LINKING MOVEMENT DYNAMICS TO ECOSYSTEM STRUCTURE: SUCKERS AS ECOSYSTEM ENGINEERS

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LINKING MOVEMENT DYNAMICS TO ECOSYSTEM STRUCTURE: SUCKERS AS ECOSYSTEM ENGINEERS

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There is substantial evidence that animals can engineer ecosystems, but little attention has been given to how movements of engineering taxa may modulate their effects on ecosystem parameters and generate heterogeneity. Spatial and temporal heterogeneity in resource availability plays an essential role in structuring many ecosystems. A wide variety of organisms may contribute to environmental heterogeneity and ecosystem engineers are particularly likely to change the spatial and temporal distribution of resources within ecosystems by creating or altering local habitat structures, through substrate bioturbation, or by transforming the chemical and light environment. Ecosystem engineers can control the spatial and temporal distribution of resources and movement by engineers within an ecosystem may transport resources across boundaries and distribute engineering effects. Movement patterns of fishes may cause physical changes to stream habitat though nesting or feeding, both of which often vary in space and time. To understand how movement can modulate the influence of an ecosystem engineering fish, I investigated 1) movement patterns of the Sonora sucker, *Catostomus insignis*, and desert sucker, *Catostomus clarki*, on several spatial and temporal scales, 2) the direct and indirect engineering effects of Sonora suckers on streambed heterogeneity (divot creation) and sediment export, and 3) the effects of fish-generated surface roughness on near-bed flow patterns, retention of coarse particulate organic matter, and invertebrate habitat.

I used stationary antennas and PIT (passive integrated transponders) tags to monitor

short-term and small-scale individual movement and population turnover within a 150-250 m reach and a portable antenna system to assess large-scale, longer term movement and home range in a > 4 km reach of the West Fork of the Gila River, New Mexico, USA from 2008 to 2010. I found that both species of suckers exhibit distinct diel movement patterns, spending daylight hours in refuge habitats (typically deep pools) while moving into shallow habitats at night to feed. While a large number of tagged fish used the stationary antenna reach, only a subset of these fishes was consistently present. The population size of the focal pools was variable, ranging from 12 to >45 individuals (approximately 0.06 to 0.22 individuals/m^2). Population turnover rates were variable from day to day, ranging from 0 to >65%. Although some individuals spent the majority of their time within the focal reach, most made extended departures (one or more days) from their home pools. Many individuals displayed substantial fidelity to a particular daytime refuge habitat despite forays elsewhere, returning to the focal reach for the duration of the study. At the reach scale, fish were generally mobile and typical home ranges exceeded 300 m, but about 25% of individuals were only ever detected in a single habitat segment. I observed increased movement after spates caused by summer monsoon rains, and fish used areas of the stream differently under high and low flow conditions. Individuals predominantly used major refuge habitats, but during high flow periods, fish often used small refuge sites with more limited overhead cover. Fish moved more between years than within years, but a subset of individuals was found in the same locations from year to year. Movement behavior did not appear to be a fixed trait for an individual, and many individuals exhibited both stationary and mobile behavior among years.

Feeding by suckers creates disturbance in soft sediments that are patchy in space and time. These disturbances move up to 2.4×10^4 cm^3 of sediment per square meter per week in locations that are up to hundreds of meters away from sucker daytime refuges. The diel cycles in

feeding activity (*i.e.,* nocturnal digging in benthic substrates) caused pulses in suspended sediment that comprise up to 34% of the daily suspended load of a stream reach. Sediment export due to fish activity made up a substantial proportion of the sediment transport from the stream reach as a whole, particularly during moderate to low flow periods. Fish create a complicated and relatively long-lived honeycomb of depressions (divots) and plateaus as they forage for invertebrates in soft substrates, physically roughening the sediment-water interface. Divots act as traps for coarse particulate organic matter and are rapidly colonized by different invertebrate taxa and at greater biomass than are found in adjacent undisturbed sediment. The surface roughness created by fields of divots, as well as the structure of the divot itself, modifies small scale flow patterns near the streambed. Divots showed increases in turbulent stress associated with a shear layer forming between the outer channel flow and the cavity flow within the divot. Stokes number scalings of coarse particulate organic matter suggest retention in the divot is due to inertial effects caused by streamline curvature, despite increased turbulence in the near bed region. The cavity flow within a divot further concentrates particulates in an upstream corner eddy.

In the Gila River sucker system, the timing and location of movement by fish modulates effects on the ecosystem and consequently engineers generate heterogeneity in resources in space and time. My findings suggest that understanding movement patterns can allow us to better assess the modifications engineering organisms make to spatial and temporal distribution of resources within the ecosystem.

BIOGRAPHICAL SKETCH

Michael Thomas Booth was born on 18 December, 1981 in Mountain View, California to Marianne and Michael Booth. He attended Sacred Heart Elementary School in Saratoga, California. During his childhood, Michael developed a strong affinity for natural areas, frequently camping, hiking, and fishing throughout California, and he fell in love with watching and catching both freshwater and saltwater fishes. From 1998 to 2000, he ran Bear Creek Custom Rods, a custom fishing rod building business, out of his home in Boulder Creek. Michael attended Bellarmine College Preparatory in San Jose, California, where he excelled in history, English, and ceramics. He then attended the University of California, Santa Cruz, where he was a Regent's Scholar and pursued a Bachelor of Science in Ecology and Evolutionary Biology. During his time at UCSC, Michael participated in a variety of field and laboratory research projects, including work tracking the movement of sculpins in the intertidal, age and growth of flatfishes in local estuaries, population dynamics of leaf-eating beetles, and the geomorphology of an ice-dammed lake in Alaska. During summer 2003, Michael was the Eugene K. Polk fellow at Grand Canyon National Park, where he managed the exotic plant management program. For his senior thesis, he studied the negative impacts of mosquitofish on freshwater invertebrate communities, for which he received highest honors in the major. Michael then moved to Arizona State University in 2004 and University of Minnesota in 2005 to work with John Sabo, Jacques Finlay, David Post, and Theodore Kennedy managing a project investigating the controls of food chain length in stream ecosystems and performing field work throughout the United States. In 2005, Michael started his PhD in Ecology and Evolutionary Biology at Cornell University and received an NSF IGERT Fellowship in Biogeochemistry and Environmental Biocomplexity. Michael began his field research investigating the role of fish in desert streams in Arizona during

summer 2006, but evacuation due to massive flooding at his field site caused an early and unexpected end to his first field season. He returned to Arizona in 2007 to continue pursuing promising leads from the previous summer, but a combination of floods, experimental failures, and logistical impossibilities led to a slight shift in focus from the direct effect of fish on ecological processes to work investigating the movement patterns of suckers. In 2008, Michael received a NSF DDIG entitled: "A question of context: The ecosystem role of catostomid fishes in Southwestern (USA)". From 2008 to 2010, Michael moved his field work to the upper Gila River of western New Mexico, where he integrated studies of movement patterns with the ecological role of suckers in the Gila River. In fall 2008, Michael founded Rio del Oso Longboards, a custom hollow wood surfboard company, and began building surfboards part time. Michael served as a conservation scientist from 2009 to 2011 for the NSF-funded program "Crossing Boundaries", a program that provides middle and high school students with knowledge, skills, motivation, and inspiration to use information and communication technologies in addressing biodiversity conservation issues in local and international contexts. The following work is the culmination of Michael's Ph.D. research.

I dedicate this work to the fishes of the Southwest, in the hopes that future generations of scientists will have the opportunity to study these magnificent creatures in their native homes.

ACKNOWLEDGMENTS

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In addition to those who directly assisted with this research, my Ph.D. would not have been possible without the outstanding support and friendship of many people at Cornell and beyond. Interactions with the amazing folks in the E231 office (a cast including David Cerasale, Paulo Llambias, Joe Simonis, April Melvin, Marissa Weiss, Morgan Mouchka, Erica Larson, Findley Ransler, Chris Dalton, and Ezra Lencer) exposed me to science from a broad range of perspectives, taught me far more about sperm than I ever expected to know, and gave me the opportunity to meet some awesome people. The folks of EEB made Corson Hall a good place to

spend a bit more than six years and I thank you all. Captain Caroline Turner and the good ship Furbish Lousewort made for some fabulous sailing in Cayuga Lake. The Ithaca Brewing Conspiracy (Ben, Gretchen, and Eli Heavner, Cloelle Sausville-Giddings, Heather Fullerton, Arend Van Der Zande, Cresten Mansfeldt, Madeline Galac, Sarah Short, Matt Rendina, and Annie Rowe) have shared some great beer and friendship over the years. SUP Cayuga, particularly Paul Wiech, Julie Carmalt, and P.J. Rusello were a great paddling support group and helped keep me sane during the final writing push.

Annie Rowe has been there with me through some tough times and some great ones. Her love, care, and support have kept me going throughout it all and I cannot thank her enough…particularly when she dropped everything (in the midst of finishing her own dissertation) to help me during the great egg explosion of Easter 2011, as well as tolerated the general insanity of Rio del Oso Longboards. I thank my parents for their support and particularly for their help in the field—they made a huge contribution to my research and have been consistently excited about the work I am doing.

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CHAPTER 1

Consumer movement dynamics drive stream habitat structure: suckers as ecosystem engineers

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Abstract

Spatial and temporal heterogeneity can be important components of ecosystem structure with the potential to modify ecological dynamics. Ecosystem engineers can control the spatial and temporal distribution of resources, and movement by engineers within an ecosystem may transport resources across boundaries and distribute engineering effects. Movement patterns of fishes may cause physical changes to stream habitat through nesting or feeding, both of which often vary in space and time. Here we present evidence of ecosystem engineering by the Sonora sucker (*Catostomus insignis*), a dominant native fish in streams of the southwestern United States, and show how the timing and location of movement patterns control heterogeneity in benthic substrates and in sediment and carbon export. Sonora suckers exhibit distinct diel movement patterns, spending daylight hours in refuge habitats (typically deep pools) while moving into shallow habitats at night to feed. Feeding by suckers creates disturbance in soft sediments that are patchy in space and time. These disturbances move up to 2.4×10^4 cm^3 of sediment m^{-2} $week^{-1}$ in locations that are up to hundreds of meters away from sucker daytime refuges. The diel cycles in feeding activity (*i.e.,* nocturnal digging in benthic substrates) cause pulses in suspended sediment that comprise up to 34% of the daily suspended load of a stream reach. Our data indicate that movement by ecosystem engineers can modulate their effects in space and time with implications for heterogeneity in the distribution of resources.

Keywords: ecosystem engineer, movement, heterogeneity, sediment dynamics, Sonora sucker, *Catostomus insignis*, sediment export

Introduction

Spatial and temporal heterogeneity in resource availability play essential roles in structuring many ecosystems (Kolasa and Pickett 1991, Palmer et al. 1997, Beisel et al. 2000,

Flecker and Taylor 2004, Winemiller et al. 2010). While it is often convenient to ignore heterogeneity as "noise" obscuring the signal of basic ecological processes, heterogeneity may be fundamentally important to the functioning of many ecosystems (Kolasa and Pickett 1991, Palmer et al. 1997, Hutchings et al. 2000, Winemiller et al. 2010). The agents generating heterogeneity can modify processes ranging from population dynamics to ecosystem structure (Stewart et al. 2000, Winemiller et al. 2010).

A wide variety of organisms may contribute to environmental heterogeneity, and ecosystem engineers (Jones et al. 1994, 1997, Wright and Jones 2006, Berke 2010) are particularly likely to change the spatial and temporal distribution of resources within ecosystems by creating or altering local habitat structures, through substrate bioturbation, or by transforming the chemical and light environment (Berke 2010). In terrestrial systems, digging by mammals can modify the availability of nitrogen (Tardiff and Stanford 1998), influence soil chemistry (Eldridge and Rath 2002), and increase plant species richness at the landscape scale (Tardiff and Stanford 1998, Doak and Loso 2003, Bruun et al. 2005, Wright 2009). By creating patches that differ in critical ways (e.g. nutrients or disturbance) from the surrounding habitat, engineering taxa can change landscape-level patterns of biota including which taxa are present and overall species richness.

In stream ecosystems, patchy distribution of resources in space may modify the distribution of organisms within the stream (Bernstein et al. 1991) and the patchy distribution of organisms can create nutrient recycling hotspots (McIntyre et al. 2008), with major consequences if the dominant species are lost (McIntyre et al. 2007). Changes in resource abundance over time may regulate the timing of organism life cycles or movement of organisms within an ecosystem (Hart 1981, Rowe and Richardson 2001). Grazers and their interactions with higher trophic

levels can generate spatial variability in resource biomass due to an uneven distribution of consumption in space and time (McIntosh et al. 2004, Hillebrand 2008).

Although there is substantial evidence that animals can engineer ecosystems (Jones et al. 1994, 1997, Crooks 2002, Moore 2006), little attention has been given to how long and short distance movements of engineering taxa may modulate effects on ecosystem parameters (Flecker et al. 2010) and generate heterogeneity. A classic example of ecosystem engineering is the effect of migratory salmonids, which create strong disturbances in benthic sediments and seasonally transport marine derived nutrients that may then fade when the organisms die or depart (Gende et al. 2002, Claeson et al. 2006, Hassan et al. 2008, Moore et al. 2008, Tiegs et al. 2009). Engineering taxa that are continuously present within an ecosystem may exhibit movements on shorter time scales or over more limited spatial areas, and ecosystem-level effects will be determined by the rate at which engineers colonize or abandon habitats (*e.g.,* beavers, Wright 2009). Movement may create pulsed influences as engineers use particular habitats, and the frequency and location of movement will determine which habitats are influenced and when. Movement patterns of ecosystem engineers may modify the size and distribution of habitat patches, dictate the level of connectedness between habitat patches, and link processes over larger spatiotemporal scales (Statzner et al. 2003).

Over short time scales, movement of key organisms can influence the flux of resources within and among ecosystems. For example, diel migration by zooplankton in lakes and the ocean may create substantial flux of carbon, nitrogen, and phosphorus between surface and deep water, moving far greater amounts of these resources than passive transport alone (Wright and Shapiro 1984, Longhurst et al. 1990). Daily feeding migration by geese transports nutrients among habitats, potentially modifying water quality in ponds and wetlands (Kitchell et al. 1999).

Moore's (2006) conceptual framework suggests that the importance of ecosystem engineers is controlled by body size, density, and engineering behavior. We suggest that this framework must also include movement patterns as a critical component of the modifications made by engineering organisms to the spatial and temporal distribution of resources within an ecosystem.

In permanent streams of the southwestern United States, the native fish fauna is often dominated by benthic feeding taxa, particularly suckers (Catastomidae). *Catostomus insignis*, the Sonora sucker, is the dominant fish species in many streams (up to 90% of biomass in our study system, the West Fork Gila River, Chapter 2). Sonora suckers are capable of significant movements (we observed up to 2900 m/day), and appear to have strong impacts on benthic processes in these streams. *C. insignis* is described in the literature as a pool dwelling fish (Minckley 1973), but suckers forage widely at night over the entire stream including extremely shallow areas. Movements between daytime refuges and nocturnal feeding grounds, as well as larger scale seasonal movements among habitats, have important implications for the timing and distribution of fish effects in the ecosystem.

We hypothesized that feeding by fish creates local patch-scale variation in substrate disturbance and modifies downstream export of sediment and carbon, particularly during periods of low stream flow. To understand how within-stream-reach movement can modify the ecosystem-level effects of fish feeding, we used passive integrated transponder (PIT) tags to monitor the movement of individual fish on several spatial and temporal scales. These movement measurements were combined with a series of observational studies examining how suckers influence sediment dynamics and carbon flux from the stream ecosystem during moderate to low-flow periods. Our results indicate the timing and location of movements by

ecosystem engineers such as suckers influence environmental heterogeneity with noticeable impacts outside of the habitats where organisms are typically observed.

Methods

Study species and location

The Sonora sucker *Catostomus insignis* occurs in a broad range of streams throughout the desert Southwest (Minckley 1973) where it is currently abundant but declining in numbers (U.S. Fish and Wildlife Service Species of Concern). *C. insignis* feeds on invertebrates and detritus (Schreiber and Minckley 1981), and is abundant during the day in deeper pools with restricted flow and fine substrates (Minckley 1973) where it is often found in large aggregations (> 30 individuals per pool, Chapter 2). Limited foraging occurs during the day, with most activity occurring during low light periods (night or high turbidity, see below). Fish dig holes while feeding on invertebrates in soft sediments (i.e., sand, silt, gravel) resulting in roughly cylindrical divots in the streambed (Figure 1.1), which range in size from 1 cm in diameter and 0.4 cm deep to 40 cm in diameter and 6.8 cm deep. Sonora suckers also feed on hard substrates, moving unconsolidated particles (pebbles to small cobbles) as they forage for invertebrates.

The upper Gila River is a tributary to the Colorado River that originates in the Mogollon Mountains of western New Mexico, and is one of the few remaining free-flowing (unregulated) rivers in the western US. Our study site at the Heartbar Wildlife area was located near the confluence of the West and Middle Forks of the Gila River. Annual hydrographs in the Gila River are driven by snowmelt, and the region also experiences a summer monsoon season (July-September), which can account for a substantial proportion of the total rainfall (Sheppard et al. 2002). *C. insignis* is abundant in the West Fork of the Gila, and populations have been monitored for the past twenty years at this location and over a broader spatial scale in the Gila River by the

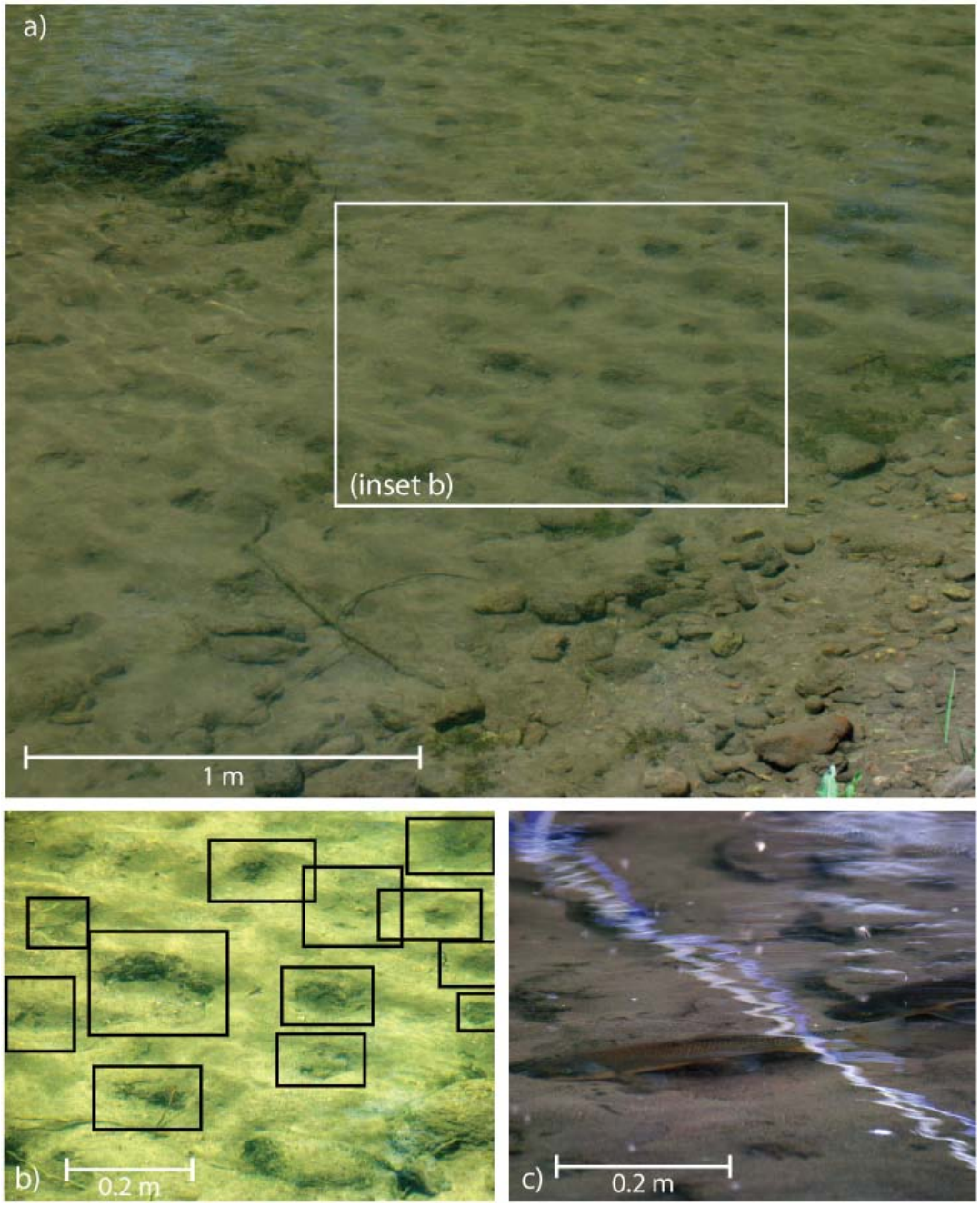

Figure 1.1. a) Feeding divots in typical fine sediments of the Gila River, showing some accumulation of organic matter. Inset b) highlights recently formed divots which often overlap with previously created depressions. c) A pair of Sonora suckers feeding in sandy sediment and creating new divots. The blue line running diagonally through the picture is the surface reflection of one of the stationary antennas. Photo credit: M. Booth

New Mexico Department of Game and Fish (Bestgen et al. 1987, D. Propst, pers. comm.). *C. insignis* typically represents the majority of fish biomass in this section of the upper Gila River (90% of the biomass in 2008; Chapter 2).

Timing and extent of fish movement

We assessed movement patterns of suckers using PIT tags and a combination of a mobile antenna and stationary antenna array (described in detail in Appendix A). Briefly, fish were captured, half duplex PIT tags were implanted in the body cavity of the fish, and fish were released in the same location where they were captured. We tagged 450 *C. insignis* within a 1.8 km reach of the West Fork Gila River from 2008 to 2010 (May to July). We mapped the tagging reach using a GPS unit (Garmin Vista Cx, Garmin International, Olathe, KS), characterized habitat (e.g., pools, riffles, runs) and substrate types, and created a GIS map using Manifold 8.0 (Manifold Software Limited, Hong Kong) to enable us to measure movement distances within the stream and estimate the areas of different habitat types.

Implanted PIT tags were detected using either stationary antennas that continuously recorded the passage of tagged fish past a fixed location in the stream, or a portable antenna that was moved within the stream to scan habitats for tagged fish. Combining these methods allowed an in-depth description of the timing of fish movements and their use of particular habitats as well as the overall spatial extent of these movements. We collected weekly position data using the portable antenna within a 2-4 km reach during May through July 2008-2010. In 2009 and 2010, we installed eight continuously recording stationary PIT antennas at the breaks in a riffle-pool-riffle-run-pool-riffle section of stream, allowing detection of animals entering or leaving the pool, moving into shallower water, or moving between pools (Figure 1.2). We collected 65 days of data during 2009 and 28 days during 2010.

Ecosystem variables

Daily discharge has been recorded on the lower Gila River (downstream approx. 80 km, USGS gauge #09430500) from 1927 to the present. In addition, during the 2010 season, we recorded water level at one location in the study reach every five minutes using Hobo water level loggers (Onset Corp, Pocasset, MA) and developed a rating curve during the sampling period to estimate discharge (Gore 2007) and establish a regression with discharge values from the long term USGS gauge site. Light and temperature were measured using a Hobo (Onset Computer, Pocasset, MA) temperature and light logger.

Divot distribution

To estimate the overall distribution of feeding divots, we performed weekly surveys within the 2 km focal stream reach. In all habitats that contained sand and silt patches we estimated divot density using two transects with four quadrats each (Figure 1.2). Within each 0.25 m^2 quadrat we counted all divots and measured the diameter and depth of four representative divots. We calculated the volume of sand displaced by the creation of the divot using the approximation of a cylinder, and scaled up to the quadrat level by multiplying the average divot volume within the quadrat by the total number of divots observed. We estimated the minimum distance to major fish refuge sites (locations with consistently >10 individuals detected) using the GIS map described above.

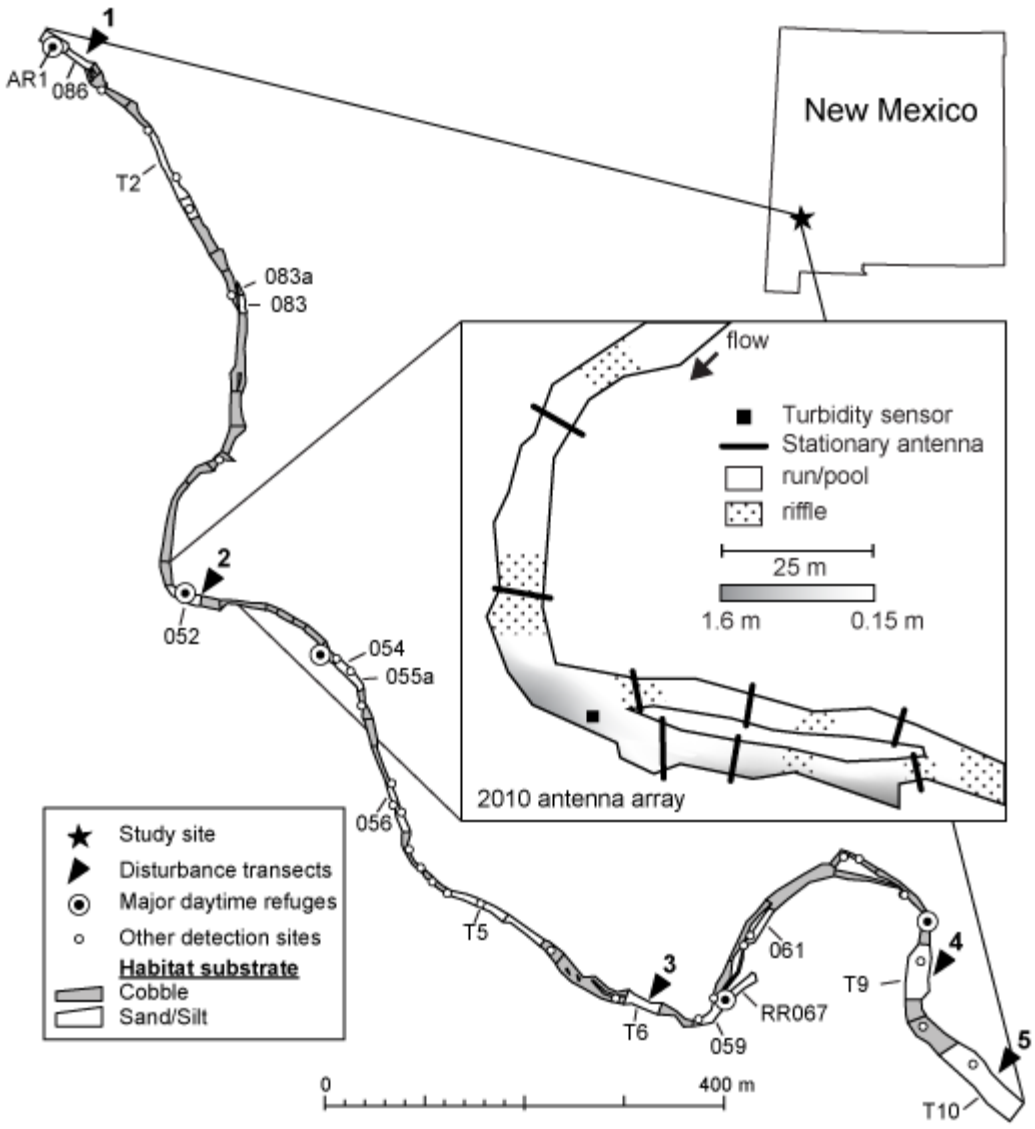

Figure 1.2. Map of the study site, including locations of 2009 disturbance transects and divot surveys (text labels indicate survey transects, see Appendix B), major daytime refuges, and the distribution of substrate types. Inset shows the 2010 stationary antenna array, and location of the turbidity sensor. The locations of the four upstream antennas in the 2009 stationary array were similar to 2010, but had to be adjusted due to changes in the channel morphology. The four downstream antennas were located approximately 150 m further downstream in 2009.

Consequences of divot formation

Due to the high prevalence of divots and the high frequency of their creation (i.e., new divots on top of old divots, so that it was unclear when a patch of habitat had last been disturbed), it was not possible to estimate directly how divoted sediments differed from those that were undisturbed. Instead, we estimated how divots change organic matter retention and invertebrate abundance in the streambed using artificially created divots made from 120 mL specimen cups (0.02 m^2 opening). At each of three sites in 2010, 20 cups were placed so the opening was flush with the surface of the stream bottom in a four by five array, with five cups collected at each sampling interval of 1, 3, 5, and 10 days. At each of the three locations on day 5, five replicate sediment samples were collected by quickly scooping sediment in a specimen cup to compare divot samples with background organic and invertebrate content. Samples were immediately frozen for processing in the laboratory. Each sample was slowly thawed and then filtered through 1 mm, 250 μm, and 45 μm mesh filters. The 1 mm and 250 μm fractions were sorted under a dissecting microscope removing all invertebrates, then all fractions were dried at 70°C, weighed and combusted at 450 °C for 4 h, rewetted to restore water of hydration, dried overnight at 70°C, and reweighed to measure organic matter content. Invertebrate taxa were identified to major groupings to the extent possible (Chapter 4), and then dried on preweighed filters at 60°C and weighed to determine dry biomass.

Disturbance transects

To estimate how fish feeding generates heterogeneity in disturbance over space and time, we set up transects perpendicular to stream flow at five locations varying in width between 5.5 and 13 m, distributed throughout our 1.8 km study reach (Figure 1.2). Locations were selected to represent the range of fine substrate habitats present in the river. Eight to 11 quadrats (0.25 m^2)

were evenly distributed along each transect, approximately every 0.5 - 1 m. Within each quadrat, five uniquely numbered and colored (pink on one side, orange on reverse) 22 mm diameter flat washers were placed in a cross orientation centered in the middle of the quadrat, with washers placed approximately 10 - 15 cm apart. Each morning, we estimated biotic disturbance by recording whether a washer had been 1) moved, 2) flipped over, 3) buried with sediment, or 4) was now in a divot. After recording the disturbances for the quadrat, washers were returned to their original locations on the bottom, or replaced with a new washer if it was not possible to recover the original with minimal searching and disruption of the sediment. These data were used to create a semi-quantitative index of sediment disturbance as follows: each type of disturbance described above was awarded one point, and a quadrat was scored by adding together the number of disturbance points accumulated by all the washers within the quadrat. In principle, a quadrat could receive a maximum score of 20 points (4 pts/washer × 5 washers). In practice we did not observe scores higher than 12, because it was unlikely, even if fish had fed throughout the quadrat, that each washer would have experienced all four types of disturbance. Typically, quadrat scores above 4 indicated that most of the quadrat was disturbed. We monitored disturbance transects during two periods (16-25 June and 12-26 July). Return time was calculated as the average time between scored disturbances within a study period. Frequency of high disturbance was calculated as the number of disturbances with scores greater than 4 divided by the total number of observations. To quantify spatial autocorrelation, Moran's I was calculated in Program R (R Core Development Team 2010) by computing an inverse distance matrix for each transect, and then using the Moran.I function from the "ape" library. An unexpected flash flood event on 25 June ended the first study period, and deposited

approximately 1-2 cm of fine sediment and coarse organic matter over most benthic surfaces. Most washers were recovered after the flood, as there was little scouring.

Suspended sediment and turbidity

Turbidity was recorded every five minutes within the stationary antenna reach during the 2010 season using a self-cleaning turbidity probe (YSI 6136) mounted on a sonde (YSI Environmental 6600 V1, Yellow Springs, OH) located immediately downstream of our stationary antenna array. To measure suspended load and carbon export, we collected bulk water samples (approximately 10 L) every 3 h for 24 h. We collected samples from one site on three dates (the stationary antenna reach, 2009), three sites on two dates (stationary antenna reach, an additional upstream and downstream location, 2009), and one site on two dates (stationary antenna reach, 2010). In 2010, we used these bulk water samples to link turbidity values to measured suspended load and carbon export. Three replicate samples were filtered on pre-ashed Gelman A/E filters (effective pore size: 1.0 μm), and immediately frozen. Filters were returned to the laboratory, dried at 60 °C for two days, weighed, ashed at 450 °C for 4 h, and then weighed. We regressed average turbidity against our measured suspended load, and used the regression equations to estimate suspended load ($DM=0.0027702 + 0.0006257 \times Turbidity$; $R^2=0.55$) and carbon export ($AFDM =0.0011673 + 5.7741\times10^{-5} \times Turbidity$; $R^2=0.24$) for each turbidity record, multiplied by the discharge at that point. To minimize the effect of noise in the turbidity data, we used the average value from the hour prior to sampling when developing regression equations.

To describe the timing of fish movement, we used detections from the four antennas directly adjacent to the pool where our turbidity monitoring equipment was located. Our measure of fish activity was the number of unique individuals detected within the antenna array during

the one hour period prior to each turbidity record (5 min interval). Since our goal was to relate overall foraging activity to turbidity, we used this rolling time period to extrapolate activity from antenna detections. Our visual observations of fish activity indicated that fish remain out in shallow water once they leave their pool and pass the antenna array.

Because sediment load typically peaked during the night and minimum suspended load values typically occurred between 1500 and 1600 h, we calculated daily sediment loads for 24 h periods starting at 1530 h to assess the diel pattern. We calculated the total amount of sediment passing by a single point (using the turbidity-sediment regression and discharge) for each 5 min interval, and summed all values for each 24 h period. Baseline suspended load was calculated as the minimum turbidity value for the day, extrapolated to the entire 24 h period. We made the simplifying assumption that fish are the primary influence on short-term changes in suspended load, and that any increase from the daily minimum value was due to fish activity. The suspended load due to fish was calculated as the difference of the total and the baseline sediment load. Time lags (the time between the peak of fish activity and turbidity) were calculated using the time series platform in JMP 8 (SAS Institute, Cary, NC), using the number of time steps that maximized the correlation between the two curves. Each sampling period was fit separately. Cross correlation values larger than $1.96 / \sqrt{n}$ in magnitude were considered significantly different from zero (Cryer and Chan 2008).

Results

Timing and extent of fish movement

Timing of movement out of refuge pools was strongly biased toward low light periods, with more than 88% of nearly 2.16×10^5 detections in the stationary antenna arrays occurring between 1900 and 0600 hours (Figure 1.3; summary in Appendix B Fig. X2). Fish passage

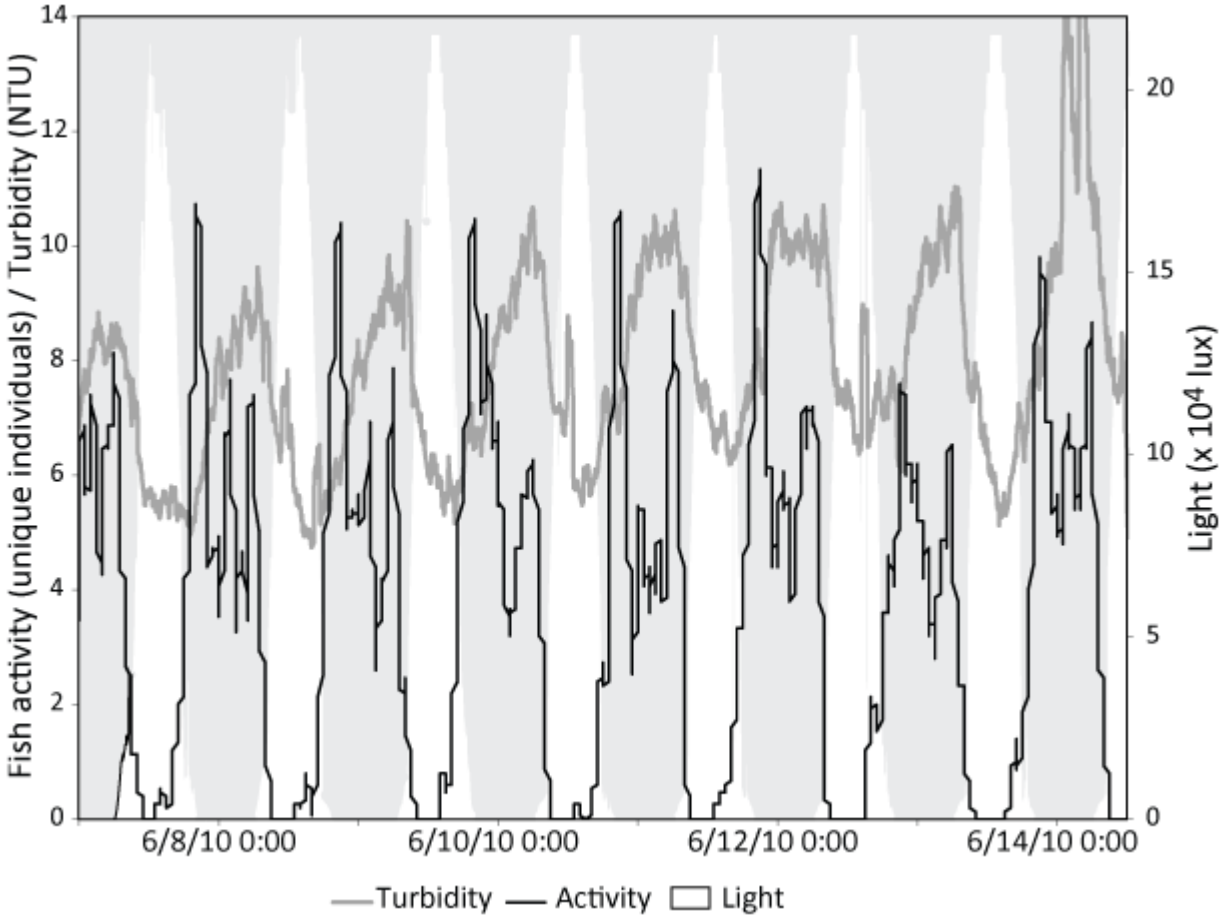

Figure 1.3. Diel pattern of fish activity, turbidity, and incident sunlight. Turbidity and fish activity values are smoothed, 1 hr rolling averages and shaded grey areas indicate evening periods when incident sunlight was not detected by sensors adjacent to the stream. Fish were rarely detected in antenna areas during the day.

through the antenna array typically peaked between 2000 and 2100 as fish left the pool for shallow water and again between 0300 and 0400, when fish returned to the pool. The timing of fish movement was consistent from day to day (see below) and among years, except during brief periods of turbid flow caused by flash floods, when fish immediately became active and remained active even during daylight until waters cleared.

Of the 450 fish originally tagged, 420 were detected at least once, and 377 more than once. Fish regularly moved among refuge habitats. Based on scans of the 4 km reach, more than 73% of the 377 fish were detected in at least one additional refuge site (mean 2.5, range 1-9 locations). Although some fish were not detected in additional refuge sites (i.e., other than their site of initial tagging), individuals within the stationary antenna reach used shallow habitats outside of their home refuge, but returned to the same pool without being detected in another refuge site with the portable antenna. Movement distances ranged from 12 to 5,400 m, with a mean of 628 m and median of 376 m. Some refuge sites consistently held substantially more fish (average number of individuals > 10, Figure 1.2) than other sites which had few fish or in which fish were only present sporadically.

Ecosystem Variables

Divot distribution

Divots were widely distributed throughout all soft-bottom sediments within the river, provided there was access from the main channel of the river, and divots appeared in newly inundated areas soon after flood events. Weekly measures of the volume of sediments displaced by divot formation in soft bottom habitats showed substantial variation within a site, but no correlation with distance to a major refuge site (Figure 1.4a). Divot density was also variable among sites and sample dates (Appendix B, Table X1). Percent cover of divots ranged from 0 to

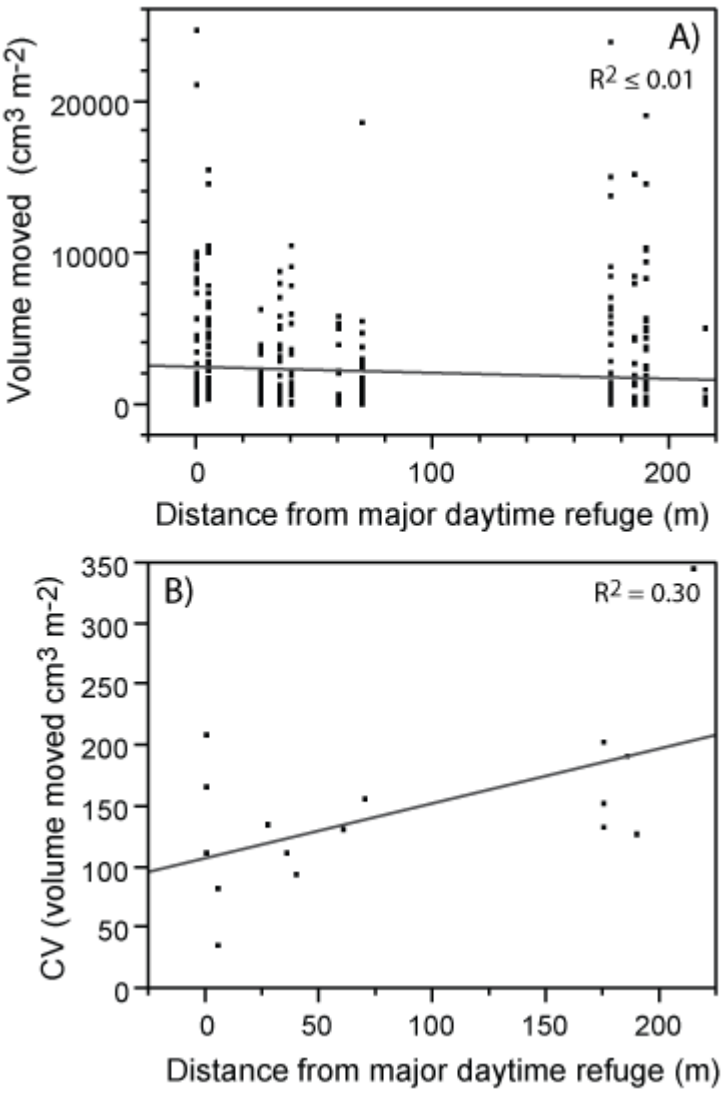

Figure 1.4. Sediment disturbance with respect to distance from a major daytime refuge habitat (see Figure 1.2). A) Each point represents a quadrat- level estimate of sediment volume moved at each divot survey site over the 2009 sampling period. The volume of sediment moved by fish was not related to the distance from major daytime refuges. B) CV values were calculated for each sample site and incorporate variation in time and among the quadrats within each site.

100% of the bottom, with sediment volume moved ranging between 0 and 2.4 $\times 10^4$ cm^3 m^{-2}. Sites further away from fish refuge sites had higher coefficients of variation (Figure 1.4b) due to greater variation within the site and over time than locations close to fish refuges. Rates of sediment displaced by divot formation averaged 260 ± 220 (mean ± s.d., range 40 to 840) cm^3 m^{-2} day^{-1}.

Consequences of divot formation

Once divots were formed, they were relatively long-lived (days to weeks), and typically filled with sediment again only due to new, adjacent, feeding activity. In general, artificial divots trapped coarse organic matter (>1mm), such as leaves and twigs, but the overall amount was variable among sites. Within one day artificial divots trapped 13.6 ± 7.9 g/m^2 (mean ± s.e.) of coarse organic matter and by day 3 organic matter increased to 37.9 ± 29.0 g/m^2. Artificial divots contained similar amounts of organic matter to neighboring sediments, but proportionally contained significantly more organic matter per unit dry mass (ANOVA $F_{1,21}$ =66.17, $p < 0.001$). We observed significantly greater biomass of invertebrates in artificial divots (0.363 ± 0.044 g/m^2) than in samples from adjacent undivoted areas (0.146 ± 0.054 g/m^2; ANOVA $F_{3,19}$ =6.17, $p = 0.004$). In addition, divots contained significantly more mayflies (1282 ± 106 [divot], 132 ± 181 [non divot] individuals/m^2; ANOVA $F_{3,19}$ =20.49, $p < 0.0001$) and elmid beetle larvae (805 ± 164 [divot], 22 ± 203 [non divot] individuals/m^2; ANOVA $F_{3,19}$ =4.65, $p = 0.0134$) than undisturbed sediment, which primarily contained dipteran larvae (chironomids).

Disturbance frequency

Relative biotic disturbance was highly variable from day to day and among transects (Table 1.1, Figure 1.5), however some transects (Transect 1 and 4) had substantially more disturbance than others (Transect 2, 3 and 5). Transect 2 (ANOVA $F_{1, 21}$= 16.01, $p = 0.0006$) and

Table 1.1. Mean relative disturbance values and Moran's I for disturbances for June and July sample periods. Negative Moran's I values were not significant, indicating a random dispersion pattern of disturbance, while positive values typically were significant, indicating clustering of like disturbance values (see Figure 1.5).

	June						July					
	Relative disturbance			Moran's I			Relative disturbance			Moran's I		
Transect	Mean	±	s.d.	Mean	±	s.d.	Mean	±	s.d.	Mean	±	s.d.
1	31	±	9	-0.13	±	0.09	30	±	14	-0.13	±	0.08
2	17	±	11	-0.04	±	0.15	6	±	3	-0.08	±	0.06
3	15	±	7	0.04	±	0.14	3	±	2	-0.05	±	0.07
4	32	±	9	0.10	±	0.18	29	±	10	0.23	±	0.07
5	10	±	6	-0.07	±	0.09	8	±	6	-0.13	±	0.07

transect 3 (ANOVA $F_{1, 21}$=43.71, $p < 0.0001$) experienced significantly less disturbance in July (the post-flood period). Disturbance return time (average time between disturbances within a sampling period, Figure 1.5) ranged between 1 day (disturbed daily) to 8 days for June, and 1 to 15 days for July. Average frequency of high disturbance (number of quadrat scores > 4 divided by total number of disturbances, Figure 1.5) was lower after the flood event in late June for transects 2 and 3, increased in transect 5, and was similar pre- and post-flooding for transects 1 and 4. Moran's I values, a measure of spatial autocorrelation, were typically negative for transects 1, 2 and 5 (Table 1.1); however, values were not significant ($\alpha = 0.05$), suggesting that disturbances were randomly distributed and not spatially autocorrelated. In contrast, portions of transects 3 (June) and 4 (both sample periods) displayed significant, positive Moran's I values (Figure 1.5), indicating spatial autocorrelation and clustering of similar values.

Effects on suspended sediments

Turbidity in the water column was greater at night than during the day (Figure 1.3), and was significantly cross-correlated with the timing of fish activity, with a time lag ranging from 1:10-2:45 (h:min; Table 1.2). Although other factors may contribute to suspended sediment loads, we did not observe other organisms with high nocturnal activity in the study area or correlated patterns in discharge or algal sloughing (M. Booth, unpub. data). There was relatively little variation in daily discharge during the study period (normally ± 10% of mean discharge) and the daily variation in discharge typically had weak explanatory power (typical $r^2 < 0.10$) for changes in turbidity values. Three dates showed strong positive correlation ($r^2 > 0.50$, $p < 0.001$) with discharge, likely due to increased sediment input from precipitation events on those dates. We did not include these dates in our suspended load and carbon export analyses because we were not able to disentangle discharge effects from those of fish activity.

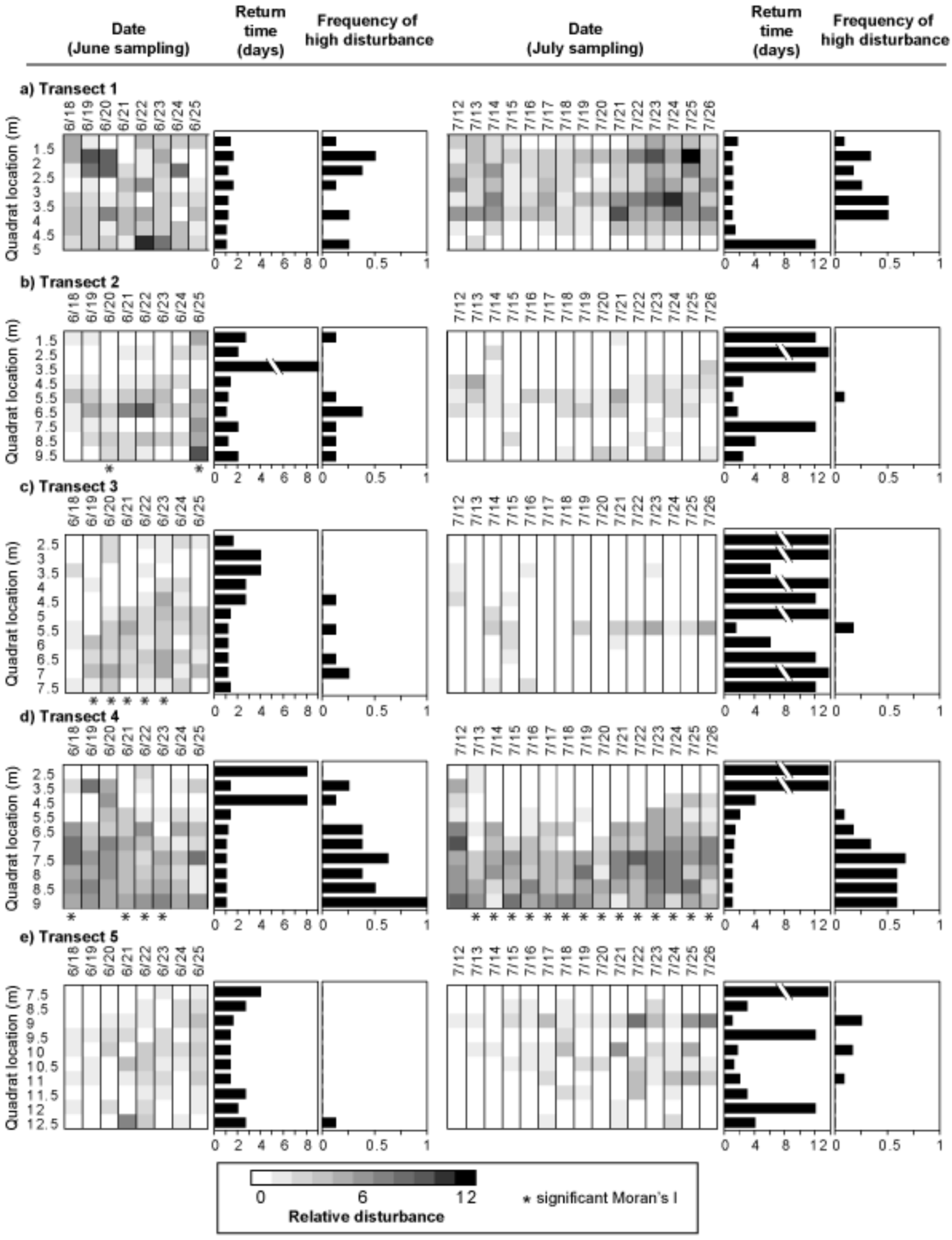
Date (June sampling)
Return time (days)
Frequency of high disturbance
Date (July sampling)
Return time (days)
Frequency of high disturbance
a) Transect 1
b) Transect 2
c) Transect 3
d) Transect 4
e) Transect 5
Quadrat location (m)
6/18 6/19 6/20 6/21 6/22 6/23 6/24 6/25
7/12 7/13 7/14 7/15 7/16 7/17 7/18 7/19 7/20 7/21 7/22 7/23 7/24 7/25 7/26
0 2 4 6 8
0 0.5 1
0 4 8 12
0 6 12
Relative disturbance
* significant Moran's I

Figure 1.5. Spatial and temporal distribution of disturbance along transects. Each shaded rectangle represents a quadrat along the transect, and darker shades represent greater disturbance. Return time is the average time between disturbance events of any magnitude for each quadrat. Frequency of high disturbance is the number of disturbances >4 divided by the total number of observation dates. Dates which had positive, significant Moran's I values, indicating nonrandom disturbance, are denoted with an * at the bottom of the column. (Moran's I values are available in Table 1.1). The June and July sampling regimes were separated by a signifcant flooding event on 25 June.

Table 1.2. Sediment and organic matter export through a cross section of the Gila River. Dry mass (DM) and organic matter (AFDM) were calculated from turbidity values for each 24-hour period beginning at 1530. Table values represent means ± s.e. for all days within the period. Lag times were calculated from cross correlation analysis and represent the time shift that maximizes the correlation between fish activity and turbidity curves. All cross correlation values were significantly different from zero based on the criteria of Cryer and Chan (2008). Fish activity was calculated from detections in stationary antennas.

Period	Lag time (h:min)	Cross Correlation	Average discharge (m^3/s)	DM (kg/day)	DM by fish (kg/day)	DM proportion due to fish	AFDM (kg/day)	AFDM by fish (kg/day)	AFDM proportion due to fish
June 1 - June 3, 2010	2:00	0.41	2.4	1953 ± 46	382 ± 37	0.20 ± 0.01	366 ± 11	46 ± 8	0.13 ± 0.02
June 4 - June 14, 2010	2:30	0.53	1.3	1025 ± 126	279 ± 31	0.27 ± 0.01	200 ± 22	35 ± 4	0.17 ± 0.01
June 16 - June 21, 2010	2:45	0.64	0.5	258 ± 22	82 ± 12	0.32 ± 0.02	62 ± 5	11 ± 2	0.19 ± 0.02
June 23 - July 1, 2010	1:10	0.41	0.4	168 ± 18	53 ± 8	0.32 ± 0.02	46 ± 3	8 ± 1	0.17 ± 0.01

Overall, there was a decrease in discharge from 2.4 to 0.4 $m^3 s^{-1}$ from June to July, with a correlated decrease in average daily turbidity (ANOVA $F_{1, 7302} = 8270$, $p < 0.0001$, $R^2 = 0.53$). We used this linear fit to subtract the effect of changes in discharge from turbidity and estimate the contribution of fish independent of discharge. Fish activity consistently contributed approximately 27-29% of the dry mass and 12-17% of the organic matter in the suspended load. However, the effects of turbidity must be experienced by other organisms within the context of changing discharge. As discharge decreased, the relative importance of fish activity grew, with the proportion of dry mass due to fish increasing from 20 to 32% and organic matter increasing from 13 to 19% (Table 1.2).

Diel bulk water sampling from 2009 and 2010 produced similar results to our turbidity records in different locations within the study reach, with peaks in suspended load higher between sunset and sunrise (Appendix B, Fig. X1). The magnitude of increase in suspended sediment during low light periods varied among dates in 2009, but did not appear to be related to changes in discharge, wind, or activity of other animals.

In order to understand the overall importance of turbidity induced by fish-feeding activity, we calculated the proportion of time that flows were low enough to observe a substantial fish effect. Based on the historical discharge record for Gila River from 1928 to 2010, we estimate that about 63% of average daily discharge values are equal or lower than 1.4 m^3/s. At this level of discharge, we estimate that at least 27% of suspended sediment dry mass and 18% of organic matter export is due to fish activity, and at lower discharge values, fish play a greater role in sediment export (Table 1.2).

Discussion

Sonora suckers are important ecosystem engineers in the Gila River with effects that vary simultaneously in time and space. They substantially modify the physical structure of benthic sediments and generate heterogeneity in disturbance of the streambed, with consequences for timing and magnitude of sediment and organic matter resuspension and export. Diel and seasonal movement patterns by the fish drive the timing and spatial extent of their effects, and indicate that movements on the order of tens to hundreds of m expand the spatial scale of the effects of these ecosystem engineers. The importance of the engineering activity is obscured under the harsh environmental conditions of high flow, as predicted by conceptual models (Moore 2006), but has the potential to be substantial when conditions are more benign.

Although fish populations have been monitored in the upper Gila basin for decades (Bestgen et al. 1987; D. Propst, pers. comm.), relatively little is known about the movement patterns and ecosystem role of this common species. Our fish movement data indicate that suckers primarily use pools as refuges during the day and make use of many other areas of the streambed to forage at night, particularly shallow areas with soft sediments. We consistently observed effects of feeding activity in areas where fish are not typically observed during the day. Effects were not related to distance from refuge within our study reach (Figure 1.4a), suggesting that distance to feeding ground for mobile taxa like *C. insignis* (at least on the order of hundreds of meters) does not regulate the strength of their effects in distant habitats. However, we noted that the further a feeding habitat was from a refuge, the more variable effects were over space or time (Figure 1.4b). This was possibly due to several causes, including 1) increased risk of predation by visual predators (e.g., birds) and higher energy expenditure due to longer distances from refuge habitats and 2) low water levels decreasing the number of fish moving through

shallow habitats separating refuge sites from shallow feeding areas within the spatial scale examined in this study.

In terrestrial systems, engineering activities that increase heterogeneity in the landscape appear to influence overall landscape-scale species richness by creating habitat that differs in a key metric (e.g., nutrients and disturbance) from unmodified habitat (Tardiff and Stanford 1998, Bruun et al. 2005, Wright 2009). In our study system, divots rapidly trap organic matter and transform a smooth streambed into a complicated honeycomb of pockets and microplateaus. The formation of divots causes substantial disturbance to the streambed (Figure 1.4a), with the magnitude of the average disturbance equivalent to turnover of the top 2 cm of the stream bottom, and creates a fluid mosaic of disturbed and undisturbed habitat patches over time (Figure 1.5). This heterogeneity has consequences for other organisms in the stream: our divot surrogates were colonized by invertebrate taxa different from those found in adjacent undisturbed sediment. These taxa (mayflies and elmid larvae) appeared to respond to the physical structure of the divot, where organic matter rapidly accumulated. Although taxa differed in the timing of their colonization trajectories (M. Booth, Chapter 4), invertebrate densities quickly increased within days to the presence of divots.

As fish fed on benthic substrates, patches of disturbance were generated over space and time (Figure 1.5). Disturbance regimes varied from daily disruption of most patches to less frequent disturbance of a small subset of patches. Furthermore, the disturbance regimes of some, but not all, patches varied before and after flooding. Such variation in the magnitude and frequency of disturbance in soft bottom sediments by fish may influence the structure of the macroinvertebrate community, both via direct consumption (Williams et al. 2003) and by the creation of new habitats through the formation of microdepositional zones (Hall 1994) such as

the divots that the *C. insignis* make while feeding. Disturbance by fish may also oxygenate sediments (Ritvo et al. 2004), while burying or re-exposing particulate organic matter and algal biofilms. Divot formation may disturb sand and sediment biofilm communities, potentially selecting for taxa that are resistant to burial, creating a heterogeneous array of algal patches, and destabilizing sediments (Peterson 1996).

In general, there was minimal spatial autocorrelation of disturbance patterns within our transects (Figure 1.5), indicating that fine scale disturbances were randomly distributed. Only two transects pre-flood and one transect post-flood showed high correlation (grouping of like values) within the disturbance transect, while the remaining transects showed random or over-dispersed distribution of disturbance. In sites with high correlation, the majority of disturbance occurred in less compacted, deeper, and higher flow portions of the transect, suggesting that environmental variation in substrate, depth, and flow patterns could modify the distribution of disturbance. During our visual observations of feeding behavior, fish appeared to evaluate substrate while feeding, and fed more intensively in particular locations while making circuits through the habitat. A likely explanation for the dispersion patterns of disturbance we observed is that in habitats that are similar in flow and substrate, fish feeding was a function of the pattern of their foraging movements, while in habitats with substantial differences in flow and substrate, the pattern of fish feeding activity was constrained to more productive locations (Figure 1.5).

It was not clear why transect locations differed in their level of disturbance (Figure 1.5), but we expect that combination of unique characteristics at each site, as well as chance, may explain these differences. Unfortunately, our temporal measures of fish abundance were too coarse to determine if changes in refuge population size influenced the magnitude or distribution of the disturbance. Because our analytical design was intended to capture small-scale variation in

disturbance, it may not have captured the overall disturbance at larger scales within sites. For example, disturbance post-flood in transect 2 (located within the stationary antenna array) was substantially lower than it was pre-flood (Table 1.1), despite the continued presence of large numbers of fish and evidence that fish were feeding throughout the site (although much less within the disturbance transect).

Flecker and Taylor (2004) showed that the effect of the density of an ecosystem engineer on resource heterogeneity follows a hump-shaped distribution with high and low density leading to homogenization of resources, and moderate densities to heterogeneous distributions. We expected a similar pattern for the Gila River, but the movement of consumers probably precluded extremely high densities from occurring and thus any great reduction of resources within a habitat. Despite extremely high numbers of large fish in the focal antenna reach (up to 65 individuals > 25 cm total length within a 24 h period), we did not observe homogenization of resources, likely because fish used alternative areas for their feeding as resources declined within the focal reach.

Ecosystem engineers may have strong direct effects (e.g., sediment movement by the suckers), but due to the timing and location of movement patterns, direct disturbance can be patchy over space and time. However, indirect effects of these engineering activities, such as sediment resuspension and settling, can be more predictable and likely impacts the entire ecosystem daily. We found that elevated sucker movement occurred during periods of low light, generating pulses of sediment movement downstream during the night that rapidly settled out during the day (Figure 1.3). These pulses of sediment may have, in turn, had consequences for the timing and feeding activity by filter-feeding insects (e.g., simulids, Hart & Latta 1986) and possibly deposit-feeding insects. It is also likely that the deposition of sediment from the water

column, which is distributed throughout the stream including areas where fish do not feed, may influence growth of periphyton and the composition of biofilms on benthic substrates (Peterson 1996). We observed 1-5 mm of sediment settling on benthic substrates daily. Sediment export due to fish activity made up a substantial proportion of the sediment transport from the stream reach as a whole (Table 1.2), particularly during moderate to low flow periods. In experimental streams, fish regulate dynamics of downstream sediment transport (Statzner et al. 2003) and other benthic feeding fish appear able to generate elevated suspended sediment loads (e.g., carp; Breukelaar et al. 1994, Ritvo et al. 2004).

A diversity of vertebrate and invertebrate taxa can influence sediment export from aquatic systems (Pringle et al. 1993, Zanetell and Peckarsky 1996, Statzner et al. 2000, Meysman et al. 2006, Moore et al. 2007, Tiegs et al. 2009). Sediment movement by organisms may be important in a variety of stream ecosystems, particularly as the activity of organisms will, in general, generate substantially different patterns of disturbance than abiotic forces (sensu Statzner et al. 2003). While the overall sediment export caused by suckers is likely relatively low compared with flood events (which are often highly turbid due to overland flow; Statzner et al. 2003) and high flows during winter snowmelt, the effects of consistent sediment pulses are quite strong during low flow periods. Based on the historical discharge record, we estimate that about two-thirds of the time, flows in the Gila are within the discharge range for which fish provide greater than 25% of the suspended sediment export. So while fish-generated sediment export may not be the single greatest contributor to the sediment and carbon budget, it represents a consistent movement of inorganic particles and organic matter through the system, as well as a major source of the particulate deposition on the stream bottom.

In the Gila River ecosystem, the timing and location of movement of ecosystem engineers modulates the effects of the fish on the ecosystem and can generate heterogeneity in resources in space and time. It is a process that seems likely to be important in other, similar systems. Moore's (2006) conceptual framework suggests that the importance of ecosystem engineers is related to their body size, density, and engineering behavior, as well as the strength of abiotic factors in disturbing the system. Our findings suggest that this framework should also include movement patterns to better understand the modifications engineering organisms make to spatial and temporal distribution of resources within the ecosystem.

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APPENDIX A: MOVEMENT METHODS

Timing and extent of fish movement

We assessed movement patterns of suckers using PIT tags and a combination of a mobile antenna and stationary antenna array. Fish were captured for tagging using electroshocking, hoop nets, and fyke nets. We used read-write half duplex PIT tags (134.2 kHz, 23 mm x 3.85 mm, RI-TRP-WEHP, Texas Instruments, Dallas, TX), which were implanted in the body cavity of the fish using a scalpel to make a small incision just below the pectoral fin and a tag injector (MK-10 implanter, BioMark, Boise, ID). We tagged 450 *C. insignis* within a 1.8 km reach of the West Fork Gila River from 2008 to 2010 (May to July). We weighed, measured, and recorded capture location of each fish and released them in the same location where they were captured. We mapped the tagging reach using a GPS unit (Garmin Vista Cx, Garmin International, Olathe, KS), characterized habitat (e.g., pools, riffles, runs) and substrate types, and created a GIS map in Manifold 8.0 (Manifold Software Limited, Hong Kong) to enable us to measure movement distances within the stream and estimate the area of different habitat types.

Implanted PIT tags were detected using either stationary antennas that continuously recorded the passage of tagged fish past a fixed point in the stream, or a portable antenna that was moved within the stream to scan habitats for tagged fish. Combining these methods allowed an in-depth description of the timing of fish movements and their use of particular habitats as well as the overall spatial extent of these movements. Our portable antenna consisted of a high performance low frequency backpack radio frequency identification (RFID) reader (Oregon RFID, Portland, OR) with slim antenna tuner board (Oregon RFID, Portland, OR) enclosed in a custom-fabricated waterproof housing; read range was approximately 50-80 cm depending on

tag orientation. In general, water clarity was sufficient to visually observe fish in water shallower than 50 cm, so we restricted our search with the portable antenna to deeper water (>50 cm) and all areas with overhead cover (e.g., roots, undercut banks), regardless of depth. During summer 2008, we collected weekly position data within the 1.8 km river reach where we tagged fish, using only the portable antenna system. In 2009 and 2010, our weekly sampling included an expanded reach 1.3 km downstream and 1 km upstream of the tagging reach to observe if tagged individuals had moved out of the original study reach.

Stationary readers employed a data logger circuit board, multiplexer (OregonRFID, Portland, OR) and RF module, control board, and antenna tuner (Series 2000, Texas Instruments, Dallas, TX). Antennas were constructed from a single loop of 8 gauge battery cable, with the top leg supported below the water surface by cable ties and nylon rope and the bottom leg buried in the stream bottom. Depending upon location in the stream, the antennas ranged from 6 to 12 m across the stream perpendicular to the flow and 0.5 to 1 m deep; read range varied between 20 and 80 cm depending on tag orientation. In 2009, a total of eight antennas were placed at the breaks in a riffle-pool-riffle-run-pool-riffle section of stream, allowing detection of animals entering or leaving the pool, moving into shallower water, or moving between pools. In 2010, eight antennas were placed to bracket a single pool and the adjacent shallow areas, which enabled better estimation of duration of use of shallow habitats (Fig. 2). We collected 65 days of data during 2009 and 28 days during 2010.

APPENDIX B. SUPPLEMENTAL TABLES AND FIGURES

Table X1. Mean and range of sediment disturbed by fish feeding at sites within the 1.8 km focal reach. Sampling sites are ordered from upstream to downstream. Missing values ("-") indicate that no data were collected because low water levels prevented fish access to the site, or fine sediment was not present at the time of sampling. All values are in cm^3/m^2.

	Sampling date														
	6/23/2009			6/29/2009			7/06/2009			7/12/2009			7/19/2009		
Site	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range
	(cm^3 m^{-2})			(cm^3 m^{-2})			(cm^3 m^{-2})			(cm^3 m^{-2})			(cm^3 m^{-2})		
AR1	5707	2502	(2262 - 10462)	3393	2461	(449 - 7349)	6017	4297	(1667 - 15441)	2758	3357	(353 - 9975)	5261	5486	(457 - 14469)
086	5576	4199	(1893 - 10369)	2794	4199	(0 - 9028)	1865	1327	(806 - 3663)	2681	2546	(206 - 5867)	3503	1725	(1862 - 5302)
T2	194	367	(0 - 843)	822	1689	(0 - 4924)	78	139	(0 - 369)	36	64	(0 - 176)	0	0	(0 - 0)
083a	-	-	-	448	421	(3 - 839)	1270	292	(1064 - 1477)	0	0	(0 - 0)	0	0	(0 - 0)
083	-	-	-	934	985	(0 - 1963)	1541	2669	(0 - 4623)	0	0	(0 - 0)	0	0	(0 - 0)
052	7622	9880	(628 - 24596)	636	760	(0 - 2029)	2187	3945	(0 - 8097)	505	572	(0 - 1023)	1347	1496	(0 - 4460)
054	3213	2437	(15 - 7326)	549	327	(0 - 984)	1535	1999	(85 - 5639)	4352	4634	(3 - 9707)	4943	3373	(1211 - 9943)
055a	5097	6655	(1468 - 18583)	394	1028	(0 - 2936)	1692	1374	(7 - 3770)	1670	1901	(51 - 5410)	2216	1570	(153 - 4675)
056	99	139	(0 - 322)	1934	5332	(0 - 15129)	3067	4008	(0 - 8430)	2168	2974	(0 - 8418)	2063	3223	(0 - 8453)
T5	1068	2539	(0 - 6249)	1053	1862	(0 - 5305)	2365	3458	(21 - 9108)	3688	4708	(0 - 13724)	8251	7699	(759 - 23804)
T6	1233	1149	(13 - 3346)	64	100	(0 - 271)	1536	1700	(0 - 3958)	828	685	(0 - 1937)	1970	2341	(0 - 6318)
059	2990	3418	(99 - 8676)	1984	2267	(0 - 5064)	1499	3165	(0 - 7938)	2562	2846	(200 - 7962)	3011	2328	(314 - 5836)
RR067	1011	361	(660 - 1433)	-	-	-	-	-	-	-	-	-	-	-	-
061	260	430	(0 - 1090)	-	-	-	-	-	-	-	-	-	-	-	-
T9	-	-	-	529	991	(0 - 2014)	4136	2468	(459 - 5738)	176	278	(0 - 585)	1692	1708	(353 - 3921)
T10	6486	7166	(430 - 19007)	3146	3424	(202 - 10311)	2147	2117	(41 - 5519)	4453	3219	(413 - 9282)	693	865	(0 - 2348)

Fig. X1. Diel seston concentrations from grab samples in 2009 (means ± s.e.). Note that the y-scale differs among dates. Shaded areas indicate dusk to dawn. Panels a-c show data from one sample location (pool with antenna array), panels d-e have two additional locations (indicated in Fig. 2).

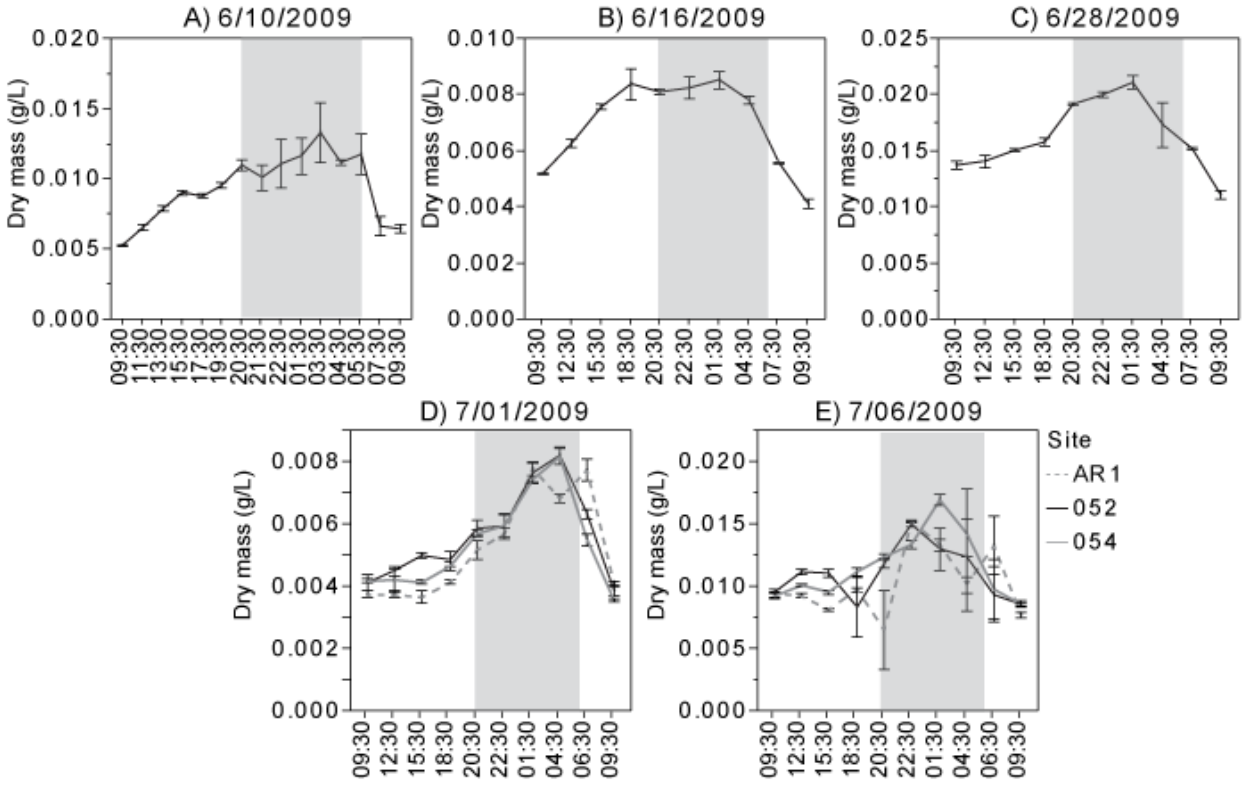
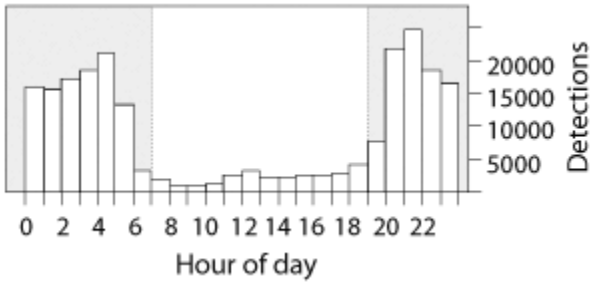


Fig. X2. Timing of all tag detections in the stationary antenna arrays for 2009 and 2010. Shaded areas indicate night.



CHAPTER 2

How fluid are fish populations? Diel movement, population turnover, and site fidelity in suckers using PIT telemetry

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Abstract

Movement of organisms within ecosystems is an important mechanism controlling an array of processes, including population dynamics, resource distribution, and biotic interactions. Recent analyses suggest that movement has two components: individual displacement (distance moved by individuals) and turnover (proportion of individuals moving). Turnover of individuals is rarely the focus of movement studies, but is important because it influences population size and structure, as well as interactions among individuals and different species within a particular habitat. We used stationary antennas and PIT (passive integrated transponders) tags to monitor individual habitat use and turnover of Sonora suckers (*Catostomus insignis*) and desert suckers (*Catostomus clarki*) within a 150 – 250 m reach of the West Fork of the Gila River, New Mexico, USA during 2009 and 2010. While a large number of tagged fish used our stationary antenna reach, only a subset of these fishes was consistently present. The population size within the focal reach was variable, ranging from 12 to >45 individuals. Turnover rates were variable from day to day, ranging from 0 to >65%. Although some individuals spent the majority of their time within the focal reach, most made extended departures (one or more days) from their home pools. Many individuals displayed fidelity to a particular daytime refuge habitat despite forays elsewhere, returning to the focal reach throughout the study. Diel or short-term movements may explain high turnover rates observed in other studies, and combined with high site fidelity, may result in the misclassification of individuals as sedentary, despite frequent movements into other habitats.

Introduction

Movement is an important mechanism regulating a variety of characteristics and processes of stream ecosystems including population dynamics (Nathan et al. 2008, Patterson et

al. 2008), predator-prey dynamics (Mitchell and Lima 2002), community structure (Matthews 1998), and habitat requirements (Teixeira and Cortes 2007, Belica and Rahel 2008). For example, the presence of top predators can lead to emigration or changes in habitat use of prey species, with potential consequences for trophic cascades (Power et al. 1985). Movement, at both large and small scales, can influence fisheries dynamics in managed systems. For example, if fish regularly move between areas with and without restricted fishing, regulations may be less effective in maintaining populations (Clapp et al. 1990, Popoff and Neumann 2005). Large-scale movements may be required for reproduction, dispersing to new habitats, or avoiding adverse habitat or resource conditions (Bryant et al. 2009, Flecker et al. 2010, Young 2011). Small-scale and short-term movements can provide opportunities for individuals to avoid predation risk or maximize foraging opportunities (Smithson and Johnston 1999, Gowan and Fausch 2002, Belica and Rahel 2008), and are particularly important in heterogeneous ecosystems like streams, where it is possible to access patches of differing quality within relatively small areas. In addition, movement dynamics (e.g., immigration and loss) can be used to assess habitat quality for fish taxa and appear to provide a more reliable assessment of habitat suitability than traditional density—quality relationships (Bélanger and Rodriguez 2002).

Although biologists have recognized that some fishes make diel migrations between habitats (e.g., feeding and refuge areas), studies have typically focused on a few individuals (Young 1999, Crook et al. 2001, David and Closs 2003, Vokoun and Rabeni 2006) or the fish community as a whole with little information on individual behavior (Reebs et al. 1995, Comeau 1998, Pierce et al. 2001, Arrington and Winemiller 2003). To our knowledge, no study has examined diel or small-scale movements for a substantial portion of the fish population with information on individual behavior. Historically, the dominant paradigm of stream fish

movement was that adult fish are typically sedentary and occupy a restricted home range (Gerking 1959, Gowan et al. 1994); however later work suggested that fish populations are often composed of a mixture of sedentary and mobile individuals (Gowan et al. 1994, Rodríguez 2002).

Recent analyses suggest that population-level movement has two components: displacement (distance moved by individuals) and turnover (proportion of individuals moving) of individuals (Schrank and Rahel 2006). The dynamics of individual turnover deserve more explicit consideration in movement studies, because they influence population size and structure for a particular habitat. High turnover has been assumed to indicate high mobility, but if home ranges are small, many individuals may leave a particular habitat (high turnover) but not move far (Rodríguez 2002). Some individuals may have a primary home habitat (e.g., pool), but make occasional forays into distant locations, while others may consistently move throughout the stream. There is evidence that individuals may exhibit fidelity to a particular habitat (Steingrímsson and Grant 2003), display home range shifts over time (Crook 2004), or have large home ranges incorporating multiple habitats. However, more studies are needed to measure the degree to which behavior patterns vary within fish populations or among species. More information would be valuable about how habitats are used, daily movement patterns and the turnover of individuals within habitats, and how these metrics may change under different environmental conditions. Even for well-studied taxa like salmonids, turnover rates and movement patterns can be variable among individuals and streams (Rodríguez 2002), and it seems likely that more distantly related fishes will show an even broader range of variation. Understanding the behavioral ecology of fishes and particularly the relationship of movement

behavior to habitat and abiotic factors is critical for furthering our understanding of fish movement dynamics and applying these findings to conservation management.

Until recently, tracking movements of individuals at a population scale has been difficult—radio telemetry is typically limited in the number of individuals (due to cost, limited signal frequencies, and the logistical challenge of tracking many fish simultaneously) and techniques that require physical recapture (e.g., electroshocking) are limited in the frequency and scale of sampling (Lucas and Baras 2000). Remote detection of passive integrated transponder (PIT) tags allow low cost, long-term monitoring of movement patterns of large numbers of organisms within small stream ecosystems (Zydlewski et al. 2001, 2006). Developments in PIT telemetry such as portable and stationary *in-situ* antennas allow investigation of fish behavior at high resolution over small spatial and temporal scales for large numbers of individuals (Burns et al. 1997, McCormick and Smith 2004, Roussel et al. 2004, Quintella et al. 2005, Bubb et al. 2006, Linnansaari et al. 2007, Teixeira and Cortes 2007, Enders et al. 2007, Breen et al. 2009, Johnston et al. 2009, Hewitt et al. 2010). Depending on the antenna design and deployment, it is possible to address questions such as fish passage through barriers (Compton et al. 2008), microhabitat use (Teixeira and Cortes 2007, Johnston et al. 2009), site visitation frequency (McCormick and Smith 2004), as well as migratory behavior (Zydlewski et al. 2006).

Movement provides important linkages among populations and habitats and there is a strong need to understand how native species move within the landscape in order to conserve appropriate habitat to maintain fisheries. The movement patterns of many common fishes in the American Southwest are poorly understood (Bestgen et al. 1987), although there is a substantial body of literature for endangered taxa like the razorback sucker (Tyus and Karp 1990, Modde and Irving 1998, Robinson et al. 1998, Mueller et al. 2000, Zelasko et al. 2010). To understand

small-scale movements and population turnover, we focused on two common, large-bodied fish in southwestern US streams, the Sonora sucker (*Catostomus insignis*) and desert sucker (*Catostomus clarki*). In this study we use PIT telemetry to study the diel behavior and habitat use by resident fish in a stream, directly estimate population turnover rates within a habitat over time, and assess whether individuals exhibit day-to-day fidelity to a particular habitat during the summer season. We also use our data to investigate changes in individual behavior due to hydrologic changes (low flow and spates) and between years.

Methods

Study species

Members of the family Catostomidae (suckers) are often the most abundant large-bodied native fish in Southwestern streams. *Catostomus insignis* and *C. clarki* occur in a broad range of streams in Arizona and New Mexico, ranging from the sub-alpine White Mountains to Sonoran desert (Minckley 1973). *C. insignis* feeds on invertebrates and detritus (Schreiber and Minckley 1981), and is abundant in deep pools with restricted flow and fine substrates (Minckley 1973) where it is often found in large aggregations (>30 individuals). In contrast, *C. clarki* is an algivore that generally scrapes algae off hard substrates. Small *C. clarki* (50 mm standard length) show continuous feeding with crepuscular peaks (Fisher et al. 1981), and anecdotal evidence suggests that adult suckers of both species use pool margins and riffles during the evening (Minckley and Marsh 2009), but need more explicit investigation.

Study location

The upper Gila River is a tributary to the Colorado River that originates in the Mogollon Mountains of western New Mexico, and is one of the few remaining free-flowing rivers in the

West. Our study site at the Heartbar Wildlife area was located near the confluence of the West and Middle Forks of the Gila, approximately 3 km downstream from Gila Cliff Dwellings National Monument. Flow in the Gila River is dominated by snowmelt and the region also experiences a summer monsoon season (July-September), which can account for a substantial proportion of the total rainfall (Sheppard et al. 2002). To monitor discharge, a gauge rod was installed during the 2009 season and water level was recorded at least once daily, and more often if there was a flood event. During 2010, water level was recorded every five minutes using Hobo water level loggers (Onset Corp, Pocasset, MA) and a rating curve developed during the sampling period to estimate discharge (Gore 2007). As juveniles, both *C. insignis* and *C. clarki* are abundant in the West Fork of the Gila, but as adults *C. insignis* dominates the fish community (*C. insignis* to *C. clarki*; juveniles 0.88:1, adults 5.8:1; M. Booth, unpublished data).

Movement

We assessed movement patterns of suckers using PIT tags and a combination of a mobile antenna and stationary antenna arrays. Fish were captured for tagging using electroshocking, hoop nets, or fyke nets. We implanted read-write half duplex PIT tags (134.2 kHz, 23 mm x 3.85 mm, RI-TRP-WEHP, Texas Instruments, Dallas, TX) in the body cavity of the fish using a scalpel to make a small incision just below the pectoral fin and a tag injector to inject the tag (MK-10 implanter, BioMark, Boise, ID). We tagged 431 *C. insignis* and 119 *C. clarki* (Table 2.1) within a 1.8 km reach of the West Fork Gila River from 2008 to 2010 (May to July). Fish were weighed, measured, and released in the same location as they were captured. Capture location was recorded. We mapped the tagging reach using a GPS each season, characterized habitat types, and created a GIS map to enable us to measure movement distances within the stream and estimate the area of different habitat types.

Table 2.1. Size and number of Sonora (*C. insignis*) and desert (*C. clarki*) suckers PIT-tagged in the 1.8 km study reach of West Fork of the Gila River and the number of fish tagged within the focal pools from 2008 to 2010.

	Catostomus insignis					*Catostomus clarki*				
Tagging	Standard length			Pool 1	Pool 2	Standard Length (mm)			Pool 1	Pool 2
Year	N	Mean ± SD	Range	N	N	N	Mean ± SD	Range	N	N
2008	233	268 ± 79	(100 - 415)	65	25	73	186 ± 43	(104 - 370)	33	1
2009	174	259 ± 76	(145 - 464)	45	17	37	194 ± 37	(150 - 292)	16	1
2010	24	211 ± 49	(152 - 310)	0	10	9	210 ± 41	(153 - 294)	0	6
Total	431	261 ± 77	(100 - 464)	110	52	119	190 ± 41	(104 - 370)	49	8

We used stationary and portable antennas to track the movement of the fish through our study reach. Portable antenna methods are described in detail elsewhere (Chapter 3). Briefly, we used a portable antenna system to scan habitats for tagged fish. Our portable unit consisted of a high performance low frequency backpack RFID reader/datalogger (Oregon RFID, Portland, OR) and a custom fabricated aluminum waterproof antenna housing with a 2.5 m fiberglass pole. Tag information was displayed on a ruggedized palm computer (Meazura MEZ1000 Aceeca International, New Zealand) connected via a Bluetooth wireless serial adapter. We recorded the habitat location and detection time for each tag. In general, fish were not present in shallow water during the daytime and water clarity was sufficient to observe if fish were present in water shallower than 50 cm, so we primarily searched with the portable antenna in deeper water (>50 cm) and all areas with overhead cover (e.g. roots, undercut banks), regardless of depth.

From 18 May to 31 July 2009 and 2 June to 1 July 2010, we sampled a reach extending 1.3 km downstream and 1 km upstream of the 1.8 km tagging reach. In addition, we looked for fish outside of the full reach on one occasion; as part of the long-term monitoring program of New Mexico Department of Game and Fish, we scanned physically-captured fish (electroshocking) for PIT tags in a section 1.3 km downstream of the full reach. We also used the portable antenna to scan an additional 1.3 km upstream of the full reach to look for fish that moved up the Middle Fork and West Fork of the Gila River. For all surveys, we began at the downstream end of the reach and worked upstream. Surveys were completed within 5-8 hours. For each individual and year, we calculated home range as the maximum linear displacement between the two most distant detection locations within the individual fish's record.

PIT tags also were detected using stationary antennas that continuously monitored the passage of tagged fish past a fixed location in the stream. Stationary readers employed a data

logger circuit board and multiplexer (OregonRFID, Portland, OR) and RF module, control board, and antenna tuner (RI-RFM-008B-00, RI-CTL-MB2B, RI-ACC-008B, Texas Instruments, Dallas, TX). Readers and two sealed, 12-V deep cycle batteries (170 ampere-hours/battery) were connected in parallel and secured in streamside plastic boxes. In 2009 batteries were replaced every 2-3 days, and in 2010 batteries were connected to 120 watt solar panels with solar charge controllers. A ruggedized palm computer (Meazura MEZ1000 Aceeca International, New Zealand) connected via a Bluetooth wireless serial adapter to transfer data daily from the data logger and displayed individual tag identification, date, time of detection, and antenna ID. Antennas were constructed from a single loop of 8 gauge battery cable (BC8R-250, Metra, Holly Hill, FL), with the top leg supported by cable ties and nylon rope and the bottom leg buried in the stream bottom. Antennas ranged from 6 to 12 m wide and 0.5 to 1 m tall, and were placed in the stream perpendicular to the flow; read range varied between 20 to 80 cm depending on tag orientation. Four antennas were attached to each of the two readers, for a total of 8 antennas, and the multiplexer cycled through all of the antennas approximately 2.3 times per second. In 2009, the antennas were placed at the breaks in a riffle-pool-riffle-run-pool-riffle section of stream (Figure 2.1), allowing detection of animals entering or leaving the pool, moving into shallower water, or moving between pools. The pools (refuge sites) selected were centered within the tagging reach to maximize the number of tagged fish present and were representative of pool habitat frequently used by suckers in the Gila River, characterized by typical depths of >1 m, overhead cover (e.g., woody debris or undercut banks), and depositional sediment. High flows during winter 2009 led to substantial changes in the stream morphology, and the stationary antenna site was relocated in 2010, bracketing a single pool and the adjacent shallow areas, to

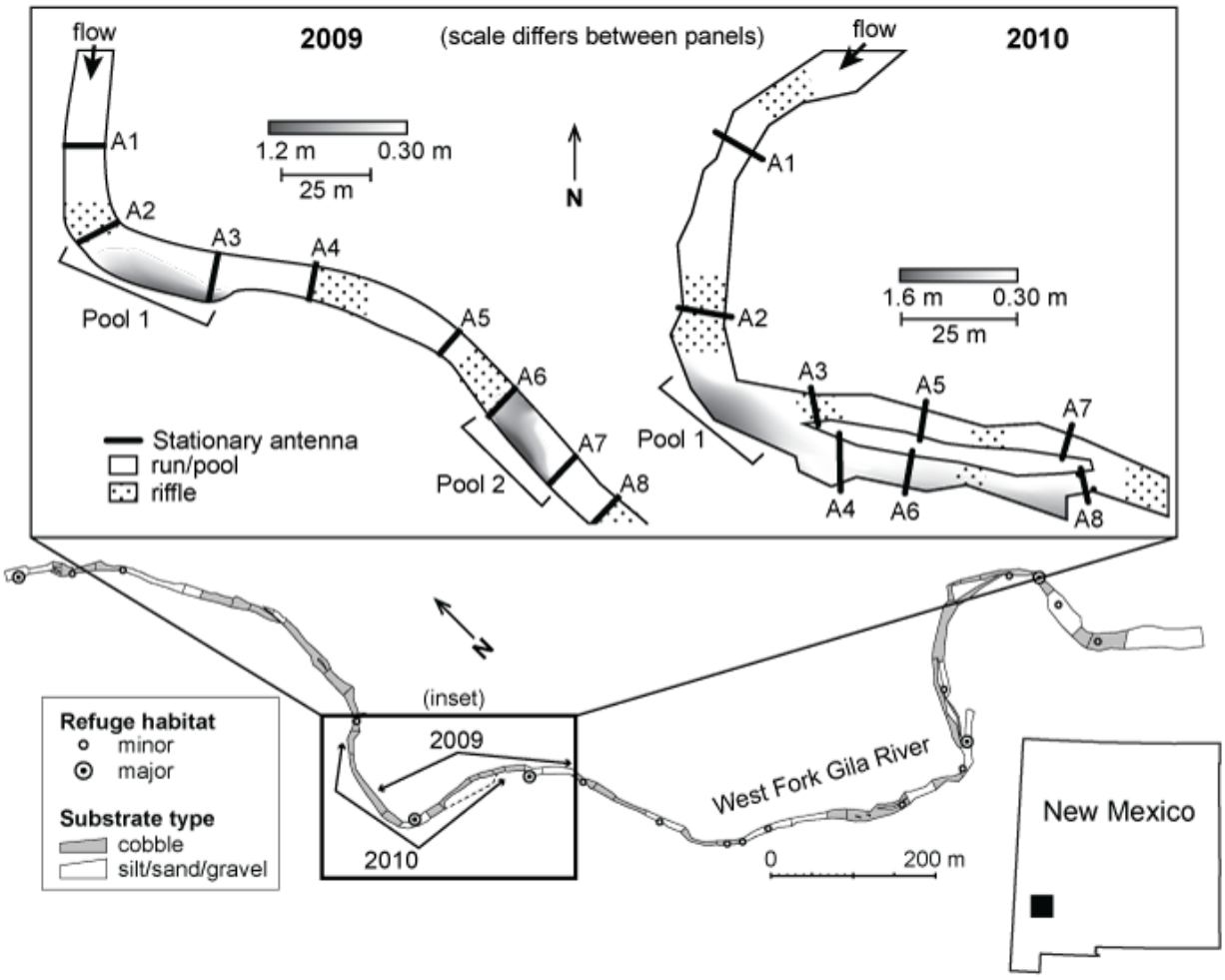

Fig 1. Map of stream substrate, consistently used refuge habitats, and location of focal stationary antenna reach. Note that the 2009 and 2010 reaches both contained Pool 1, but the overall spatial extent of the 2009 reach was larger and incorporated an additional refuge habitat (Pool 2). River morphology also changed between 2009 and 2010 (sharper bend at upstream end of reach and channel split below Pool 1).

allow for better estimation of duration of use of shallow habitats (Figure 2.1). We collected 65 days of data from the stationary antenna reach during 2009 and 28 days during 2010.

We tested PIT tag detection efficiency when antennas were installed and once during the middle of the sample period. Detection efficiency was assessed by passing a PIT tag enclosed in a neutrally buoyant container through the antenna field ten times at evenly spaced intervals across the width of each antenna. Antennas were monitored daily and retuned during the sample period when current through the antenna dropped below 1.2 amps or changed substantially (>0.2 amps). Detection efficiency was calculated by the methods of Zydlewski et al. (2006).

Analyses

Stationary antennas continuously recorded any tag within the read range for the duration that it was present in the antenna field and quickly generated large data sets. For ease of analysis and to reduce database size, we merged detections of an individual in the same antenna that were less than 2 minutes apart. For analysis of turnover and residency, we divided the reach into segments (2009: upstream-A1; Pool 1 - A2-A4; Pool 2 - A5-A7; downstream – A8; 2010: upstream – A1; Pool 1 – A2-A4; shallow side channel –A5, A7; deep side channel – A6, A8) , and classified individuals based on the last antenna where they were detected during a 24-hour period (12:00 noon - 12:00 noon) (Figure 2.1).

We categorized individuals as “transient” (< 10 days) or “frequent” (≥ 10 days) visitors to pool habitats using natural breaks in the data (the number of times individuals were last detected in either of the pool habitats). For frequent visitors to the two pools, we calculated the degree to which individuals exhibited preference or fidelity to one of the two pool habitats. We calculated

fidelity as the proportion of observations in the most frequently visited pool divided by the total number of observations for the individual.

We calculated population turnover (*T*) as the number of fish that were classified as present in the focal pools as

$$T = 1 - \left(\frac{N_i \cap N_{i-d}}{N_i}\right) \quad \text{Equation 1}$$

where *T* is turnover, N_i is the tagged population detected in the pool on the current day and the numerator is the number of individuals that are shared (intersection) between the current day *i* and *d* days prior to the current day. Daily turnover was calculated with *d*=1 for Pool 1 (30 May to 26 July 2009, 1 June to 30 June 2010) and Pool 2 (27 June to 26 July 2009). Our expectation was populations would be more similar between subsequent days but the difference would increase over longer periods. To test for a correlation between turnover and time, we calculated turnover each day for *d*=1 to *d*=24 over sampling period where all antennas were installed (27 June to 26 July 2009 and 1 June to 30 June 2010). Our definition for summer residency was that an individual was detected for a minimum of 20 sampling days within the focal pool (2009: >25 days; 2010: >20 days).

Results

Detection efficiency was high in the central antennas for each pool in 2009 (> 80%), but low in antenna 4 and 5 (< 30%) due to lower amperage from long cable runs. Due to their location in the array, missed detections in antenna 4 and 5 do not influence estimates of residency or turnover, but may have influenced our classification of behavior type. In 2010, detection efficiency was typically high (> 80%) except antenna 3 (50%). Antennas were

functional throughout the study period except for a single failure during a spate on 25 June 2009, when several antennas were displaced by flood-borne debris. Antennas were repaired and replaced within 3 hours of the spate.

Of the 550 *C. insignis* and *C. clarki* tagged between 2008 and 2010 in the 2 km reach of the West Fork Gila River, we detected 249 fish in 2009 and 102 fish in 2010 in the 200-300 m stationary antenna reaches (Table 2.2). Nearly half of fish detected within pool 1 in both 2009 and 2010 were individuals that were tagged in pool 1, and the majority of individuals observed in the upstream and downstream reaches were tagged within pool 1 and pool 2. We observed 9 individuals that were frequent (> 10 times) visitors in both 2009 and 2010 and 31 individuals that were observed at least once in both years.

Fish typically moved through antennas and into shallow water (< 50cm) to feed during the night, with crepuscular peaks in activity (Figure 2.2A-B). Some individuals made occasional forays through the antenna array during daylight hours, but visual observations confirmed that most fish were concentrated in pool habitats and under overhead cover. However, a brief spate substantially decreased water clarity from 25 June 2009 at 16:05 (zero visibility) until 27 June 2009 at 14:00 (0.5 m visibility) and fish activity continued into daylight hours (Figure 2.2C).

Individual *C. insignis* exhibited intrinsically different movement patterns as well as different responses to environmental changes like spates (Figure 2.3). However, there were several general behavior categories observed in each year. In 2009, the major behavior categories were: 1) limited forays (typically observed in only 1 antenna, with occasional longer movements), 2) regular forays (consistent movement through multiple antennas), 3) transient/directed (movement through the entire reach, with only brief visitations to the focal reach). In 2010, we

Table 2.2. Fish detected in the focal stationary antenna reach during 2009 and 2010 and the percentage of detected individuals that were tagged in that habitat. The majority of *C. clarki* tagged from 2008-2010 were captured in the upstream pool. In 2009, the focal reach included an upstream (Pool 1: antenna A1-A4) and downstream (Pool 2: A5-A8) refuge habitat. In 2010, the focal reach included one primary refuge habitat (Pool 1).

Species	2009							2010	
	Upstream		Downstream		Both habitats		Total	Entire reach	
	N	% tagged	N	% tagged	N	% tagged	N	N	% tagged
Catostomus insignis	144	49%	113	26%	91	64%	166	83	42%
Catostomus clarki	27	74%	24	4%	21	81%	83	19	42%

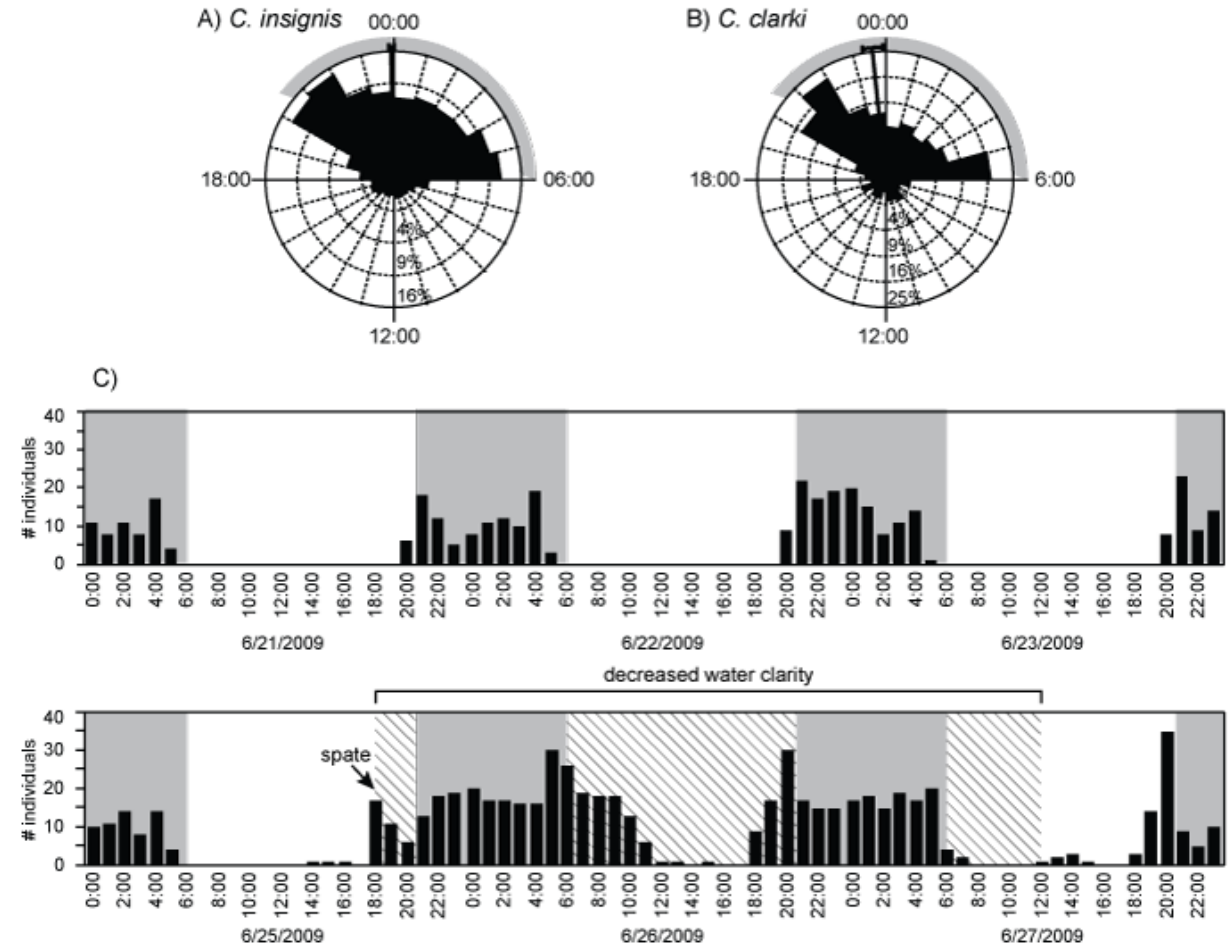

Figure 2.2 Timing of movement through stationary antennas for A) *C. insignis* and B) *C. clarki* based on all detections from 2009 and 2010. Thick, solid black line indicates overall mean and s.e. of movement timing, the grey semi-circle indicates night, and values represent the percent of observations during each time period. C) Timing of daily movements through stationary antennas before (upper panel) and during a period of decreased water clarity (cross-hatching, lower panel) following a spate in 2009. Visibility was 0 m directly following the spate gradually increasing to >0.5 m. Both *C. insignis* and *C. clarki* showed a similar response and are combined for clarity.

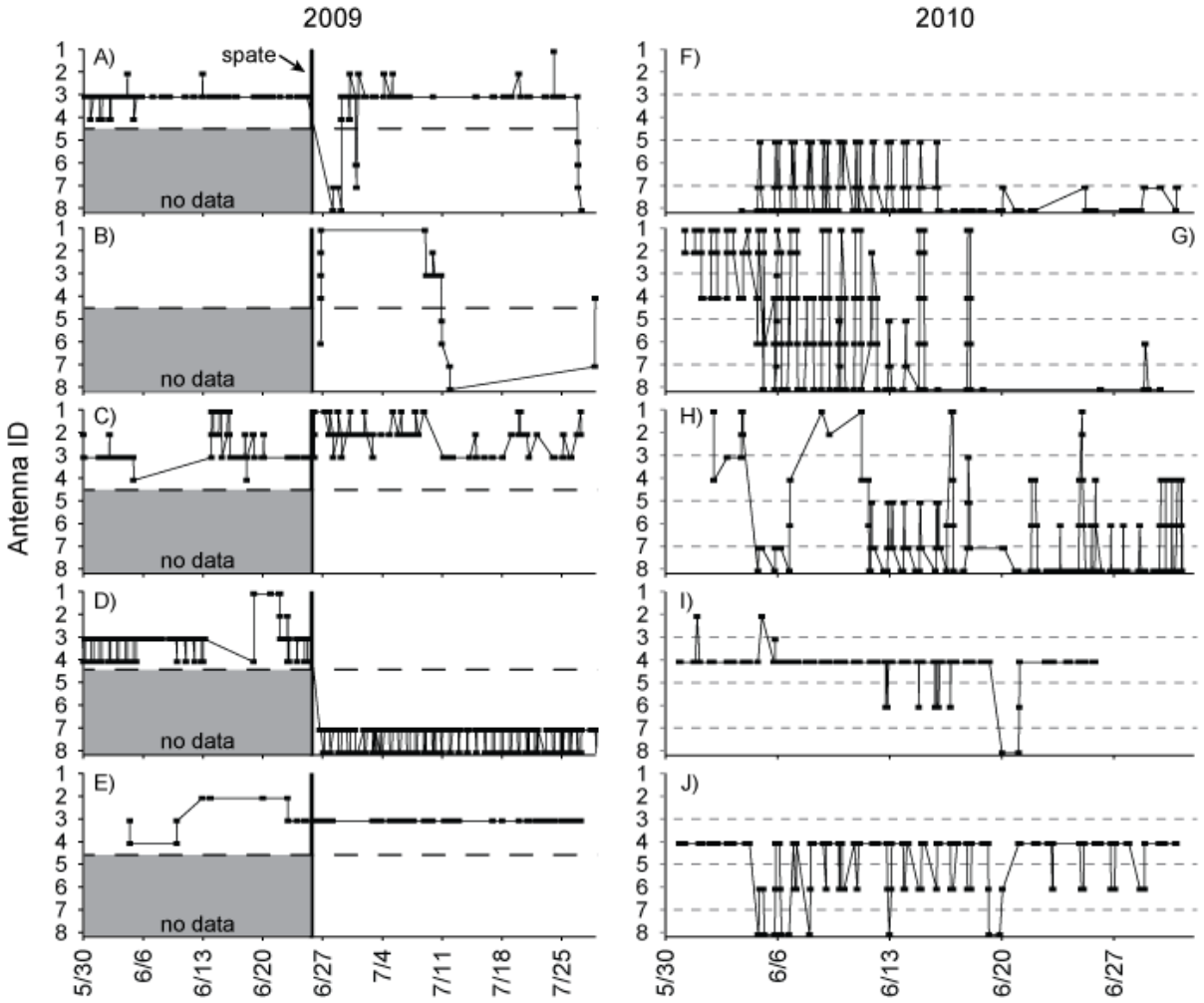

Figure 2.3. Movement behaviors for individual *C. insignis* during the 2009 and 2009 study season, highlighting major behavior categories. Dashed lines delineate the upstream antenna reach from the downstream reach (A-E) or the side channel antennas (F-J). *C. clarki* displayed similar movement behaviors. Major behavior categories: A, E, I) limited forays (typically observed in only 1 antenna, with occasional longer movements), B) transient/directed (movement through the entire reach, with only brief visitations to the focal reach), C, D, F, G,H, J) regular forays (consistent movement through multiple antennas). Some individuals made frequent forays into the shallow side channel in 2010 (e.g., H). Flood responses are shown in panels A, C, D, E.

observed similar behaviors, but additionally observed individuals that only used the side channel portion of the reach (Table 2.3). We had sufficient data for 97 individuals to determine their response to the spate in 2009. Fish exhibited several responses—individuals made a brief (< 3 day) displacement out of the reach (e.g., Figure 2.3A; 29 individuals), sustained displacement to an alternative habitat (e.g., Figure 2.3D; upstream: 32, downstream: 12 individuals), or showed no change in their activity (e.g., Figure 2.3C and 3E; 24 individuals).

In 2010, fish use of the shallow side channel habitats (A3, A5, A7) was related to discharge (Figure 2.4). As discharge and water depth decreased, substantially fewer individuals used the side channel ($F_{1,59}$=31.891, p<0.0001) when the average side channel depth was < 10 cm. We observed a greater drop in detections in A5 and A3 indicating that those that used the channel did not travel as far upstream. The number of individuals using each antenna in the main reach as a whole did not change over time, except for a slight reduction in antenna 1 as discharge decreased (ANOVA $F_{1,30}$=4.913 p=0.034).

Approximately half of the *C. insignis* and *C. clarki* were transient visitors to the stationary antenna reach during 2009, but the majority of *C. insignis* were transient visitors in 2010 (Figure 2.5A). In pool 2 (2009), transient fish were smaller on average (272 mm SL) than frequent visitors (302 mm SL; Z=2.704 df=42, p=0.007), but no differences in size were observed in pool 1 (Z=0.487, df=47, p=0.626). Most frequent visitors to the reach in 2009 exhibited strong fidelity to only one of the pools (hypothesized mean = 0.5, Wilcoxon Signed-Rank, p<0.0001; Figure 2.5B), although eight *C. insignis* and two *C. clarki* used both pools a similar proportion. Frequent visitors typically had significantly smaller home ranges than

Table 2.3. Individual movement patterns for Sonora and desert suckers, based on their entire movement record for each study year. Fish were classified as “limited” (primarily detected in a single antenna with rare excursions into other antennas), “regular” (regularly moved through at least 2 antennas), “transient/directed” (brief incursions into the study reach, often with consistent upstream or downstream trajectory) or “other”. In 2010, some individuals only used the shallow side channel of the focal reach (antenna A5, A7).

	Catostomus insignis				*Catostomus clarki*			
Year	limited	regular (side channel)	transient/ directed	Other	limited	regular	transient/ directed	Other
2009	15	82	68	1	2	13	14	1
2010	4	30 (3)	46	0	0	3	16	0

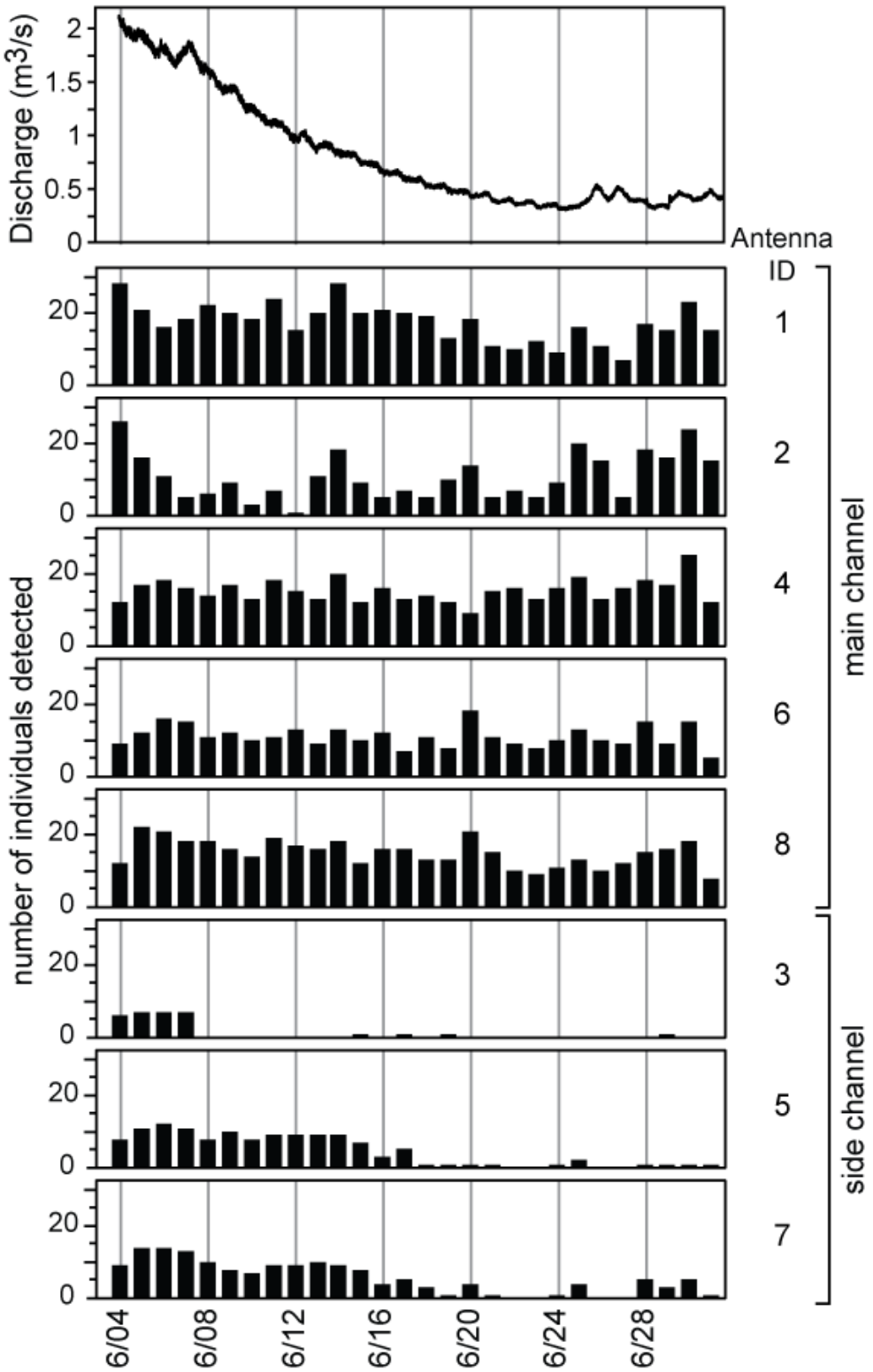

Figure 2.4. Fish use of main channel and shallow side channel habitat in relation to stream discharge. Average depth in antenna A5 and A7 was <10 cm at minimum discharge.

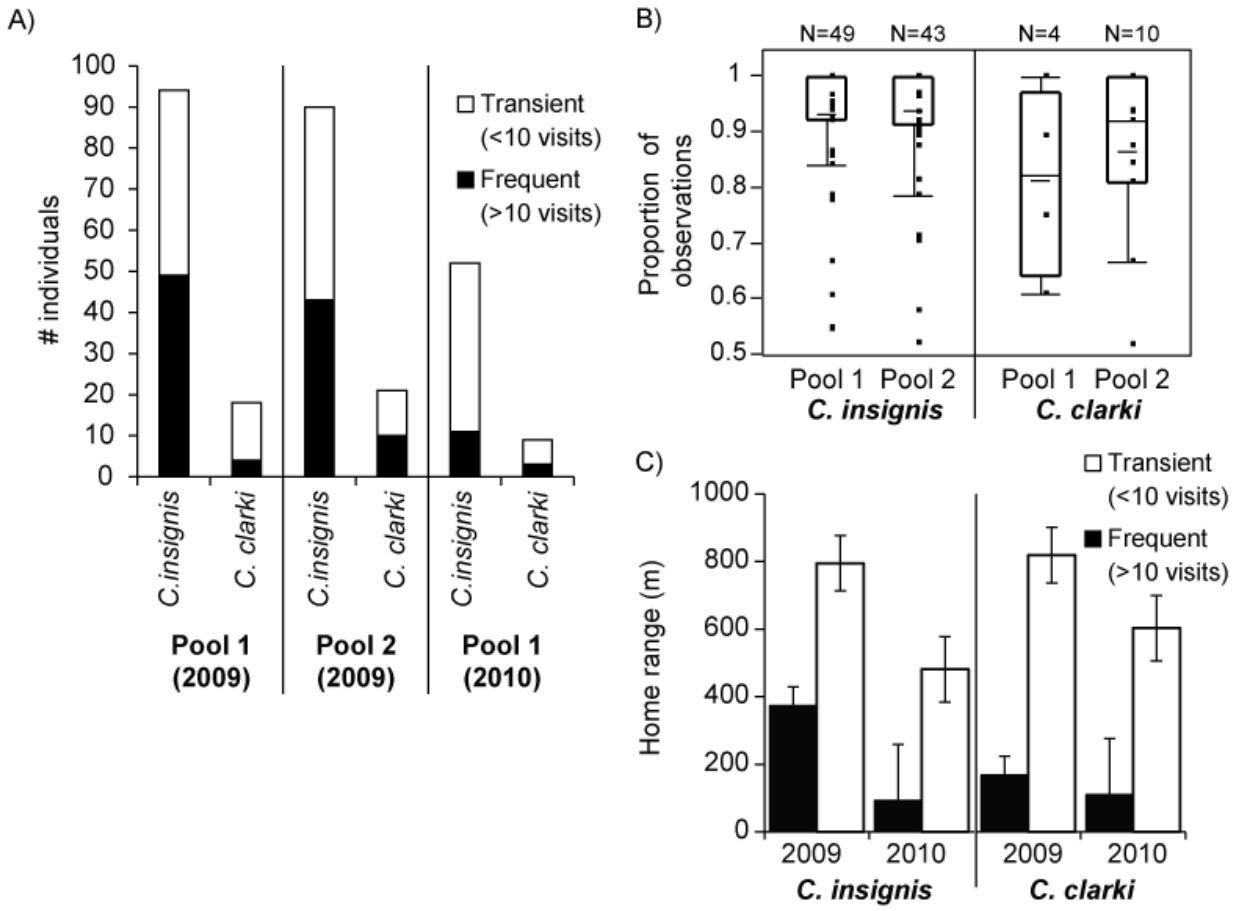

Figure 2.5. A) Proportion of Sonora and desert suckers detected within each habitat and season that were frequent (>10 visits) or transient (<10 visits) visitors to habitats within the focal reach. B) Fidelity of frequent visitors to one habitat within the focal reach in 2009. Fidelity was calculated as the proportion of total visits where the individual was detected within the more frequently visited habitat. Fidelity of 0.5 indicates equal use of both pools. Each point represents an individual fish. The ends of the box are the 25th and 75th quantiles, the line across the middle of the box is the median sample value, and whiskers are ± 1.5 × interquartile range. C) Mean ± standard error home range for transient and frequent fish.

transient visitors (*C. insignis* 2009: $F_{1,131}$=17.97, p<0.0001; 2010: $F_{1,42}$=4.0743, p=0.05; *C. clarki* 2009: $F_{1,24}$=9.473, p=0.005; 2010: $F_{1,7}$=2.966, p=0.13). However, half of the frequent and transient *C. insignis* showed relatively small home ranges (< 250 m).

Population size of *C. insignis* was more variable in pool 1 than pool 2 during 2009 (pool 1: 31 ± 10 individuals, pool 2: 33 ± 6 individuals; χ^2=14.06 p=0.002) (Figure 2.6). The number of resident fish (individuals spending >25 days within the habitat) was lower in pool 1 than pool 2 (Wilcoxon Signed-Rank, p<0.0001) and typically made up a larger proportion of the total daily population in pool 2 (pool 1: 27%, pool 2: 46%; t-test, t=18.335, df=30 p<0.0001). Daily turnover was variable in both 2009 and 2010, ranging from 0 to >60%. There was no relationship between the change in population size between days and the turnover rate (r^2<0.001) for either pool in 2009, but in 2010 turnover was positively correlated with the change in population size ($F_{1,29}$=9.887, p=0.004). In 2009, high turnover in pool 2 was partially driven by individuals moving from pool 1 into pool 2 ($F_{1,28}$=16.23, p=0.0004), but high turnover in pool 1 was not related to individuals moving from pool 2 into pool 1 ($F_{1,28}$=2.699, p=0.112). The individuals composing the population were more similar over short time scales (1-2 days) than long time scales (weeks) (Figure 2.7; $F_{3,1328}$=213.893, p<0.0001). Turnover rates were higher in 2010 than 2009.

Discussion

Small-scale movements have important implications for the structure of populations, interactions among individual animals, and the effects of individuals on the stream as a whole. We observed that both *C. insignis* and *C. clarki* made regular forays into shallow habitats during the evening and movement into and among habitats was influenced by changes in flow (e.g.,

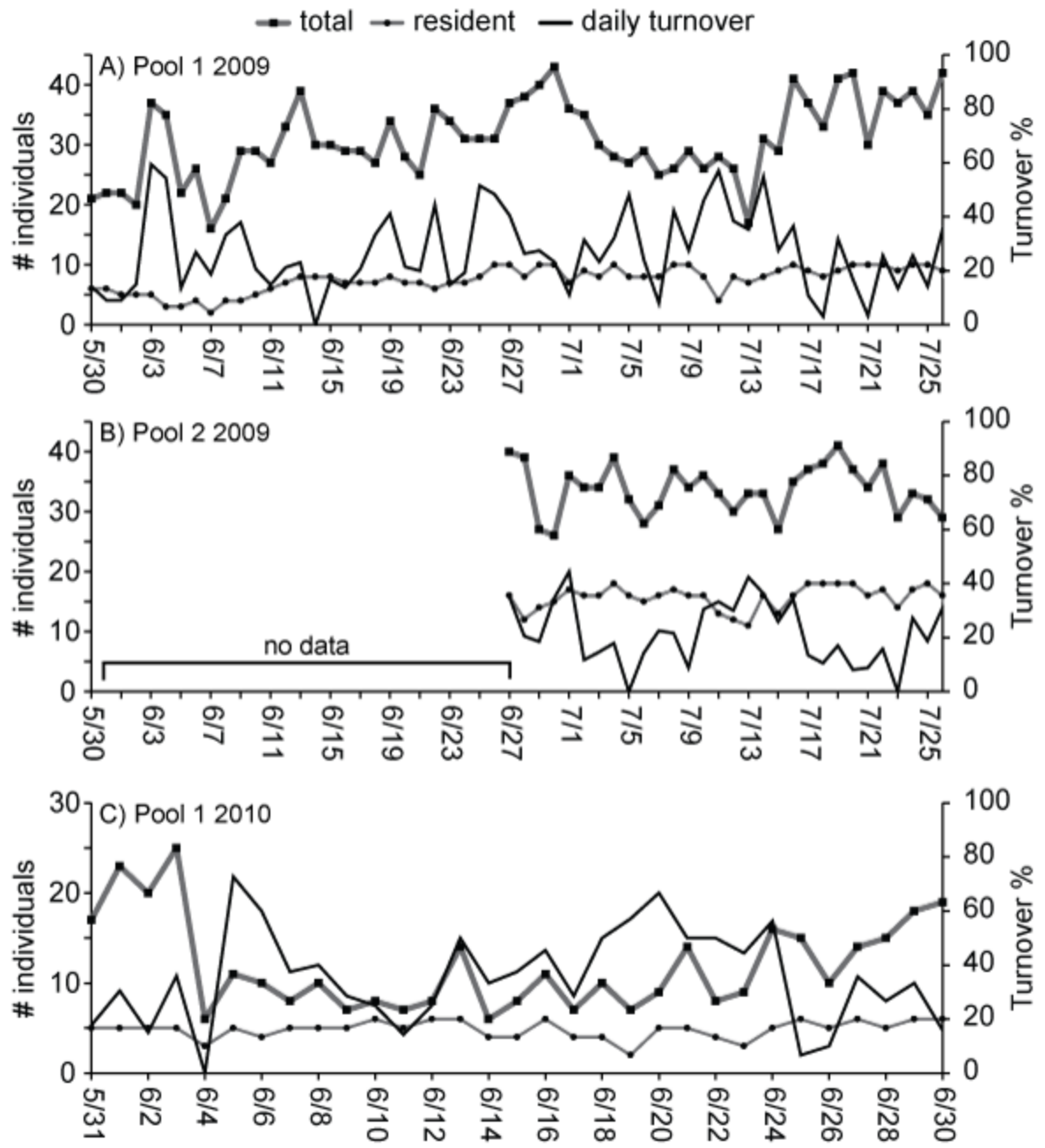

Figure 2.6. Daily turnover (see methods), number of resident fish (observed ≥25 times), and total number of *C. insignis* last observed within A) Pool 1 in 2009, B) Pool 2 in 2009, and C) Pool 1 in 2010. No data available for Pool 2 in June 2009 because antennas were not yet installed.

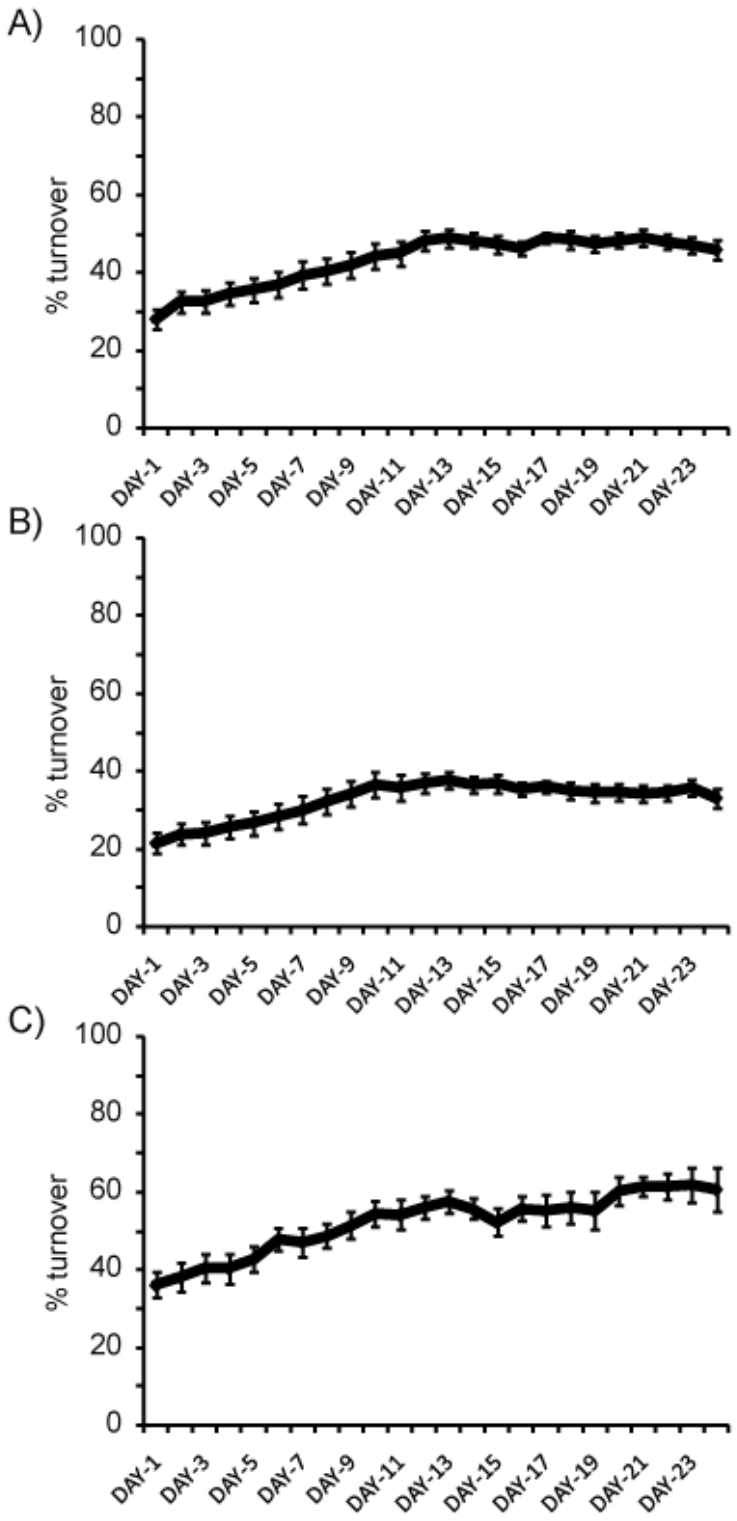

Figure 2.7. Population turnover for *C. insignis* over time, ranging from 1 to 24 days. Data points are mean ± standard error of turnover rates (see Methods) for A) Pool 1 in 2009, B) Pool 2 in 2009, and C) Pool 1 in 2010.

spates and low discharge). High rates of movement resulted in changes to population level parameters including fluctuations in population size and turnover of individuals within a habitat. Although many individuals made frequent forays outside of the refuge sites, some individuals displayed remarkable fidelity to a single focal refuge during a summer season and occasionally between years. Our results indicate that population turnover can be quite high (Figure 2.7) in stream fish populations, and that the combination of site fidelity with frequent, small-scale movement may provide a partial explanation for the observation in other systems that many adult fish appear to be sedentary.

Fish activity was concentrated during the night, with occasional forays into shallow water during the day. All of the daytime refuges occupied by fish provided substantial overhead cover and movement patterns coincided with incident light. In addition, fish activity responded quickly to changes in water clarity, with activity extending into daylight hours while water was turbid during a spate. Nocturnal behavior and response to water clarity suggests avoidance of visual predators, whose ability to capture prey is directly related to light availability and turbidity (Aksnes and Giske 1993). Although we did not observe direct predation on large fish, the presence of piscivorous birds in the area (e.g., mergansers, herons, osprey) and beak-shaped scars on fish indicate that predation risk may explain avoidance of shallow habitats during the daylight hours.

Because adult fish appear to be constrained to refuge sites during the day, spatial knowledge of the overall stream landscape may be of crucial importance for an individual (Bernstein et al. 1991, Gowan and Fausch 2002) if this enables it to make nighttime foraging forays into high resource habitats to forage and then return to refuge sites. Stream salmonids appear to monitor habitat conditions at a reach scale (100s of meters) and when large,

competitively dominant individuals are denied access to their preferred feeding habitat, many move to a new habitat rather than displace subordinate individuals within their habitat (Gowan and Fausch 2002). Due to differences in foraging behavior between salmonids and suckers, we do not expect displacement to result from interference competition between suckers (Baltz and Moyle 1984), but it seems likely that individuals may monitor conditions at the reach scale for other reasons. Indeed, we observed that individuals make similar foraging movements from day to day (e.g., Figure 2.3D, F, J), suggesting that fish may be familiar with a particular section but occasionally investigate other sections of the stream while foraging. Other species of fish, including other suckers, show similar diel movements between distinct habitats (Matheney and Rabeni 1995, Arrington and Winemiller 2003), suggesting that frequent forays out into adjacent habitats may be a common theme in stream fishes, although the extent of these movements likely varies among taxa. Foraging theory suggests that individuals should seek new habitat when the fitness increase experienced by moving outweighs the fitness realized by remaining in their current habitat (Charnov 1976, Gowan and Fausch 2002). Because fish are constrained to using refuge habitats during the daytime, the distribution of animals is unlikely to follow an ideal free distribution relative to food resources, which are likely distributed in the stream independent of refuge habitats. Assessing the environment is advantageous when the quality of the environment varies spatially and temporally, even if habitat assessment is costly (Richards and de Roos 2001). If the consumer's movement is large compared to the spatial distribution of resources, consumers that move will have more complete knowledge of resource availability and thus be able to make more ideal decisions for habitat switching (Bernstein et al. 1991).

Sucker activity, however, must account for access to food resources as well as availability of daytime refuges. Both species are capable of substantial movements within short

periods (> 1 km/day; Chapter 3) and thus can access high quality habitats distant from refuges, but potentially risk predation if they are unable to locate a daytime refuge. The preference for a particular pool we observed for frequent-visitor fish may be due to knowledge about the availability of refuge sites in the focal reach, although other explanations (e.g., minimizing energy expenditures) cannot be discounted. Other fishes (e.g., suckers, carp, catfish) appear to have home habitats from which they make regular forays (Matheney and Rabeni 1995, Crook 2004, Vokoun and Rabeni 2006) and it is possible that this behavior is common in other taxa as well. Vokoun and Rabeni (2006) suggest that some taxa, like flathead catfish (*Pylodictis olivaris*), may be less sedentary than previously thought because they move at time scales shorter than most studies can detect and show fidelity to particular locations in the stream. Similarly, Sonora and desert suckers appear to be more mobile than previously described (Bestgen et al. 1987)

High turnover of individuals (fish leaving the marking reach) has been offered as an explanation for the observation that many fish marked in mark-recapture studies often are never recaptured (Rodríguez 2002). Although stream salmonids commonly show high turnover but short movement distances (Gowan and Fausch 1996, Hilderbrand and Kershner 2000, Rodríguez 2002, Schrank and Rahel 2006), there is disagreement whether there is a consistent relationship between turnover and displacement (Gowan et al. 1994, Rodríguez 2002). Our findings suggest that individuals transiently visiting a section of stream tend to have larger home ranges than individuals frequently observed in that habitat. However, about half of the transient individuals showed small home ranges (<250 m) and half of the frequent visitors made forays to distant habitats, resulting in large home ranges (500-1500 m). So while high turnover potentially provides some explanation for fish that are not recovered in mark-recapture studies, high

turnover in our study resulted in a wide range of displacement distances and did not necessarily result in either high or low displacement. A large proportion of the population in the focal pools were transient visitors, often from locations up to several kilometers away, and individuals who frequently visited the pools also made extended forays outside of the focal antenna reach, contributing to daily population turnover.

Ranging behavior (short-term exploratory behavior) has been documented in salmonids (Gowan and Fausch 2002, Schmetterling and Adams 2004, Schrank and Rahel 2006) and is thought to be related to changing environmental conditions and resource availability (Gowan and Fausch 2002). However, displacement distances are typically limited. Salmonids typically feed on drifting invertebrates which are replenished from upstream sources and so individuals compete for relatively small feeding stations to access resources in the drift (Fausch and White 1981, Baltz and Moyle 1984). Unlike the drift, resources in patches of benthic habitat may be temporarily locally depleted due to foraging activity and so benthic feeding fishes may need to move greater distances to access foraging areas with adequate food resources. Catostomids are predominantly benthic feeders and in large rivers, other species like the northern hog sucker (*Hypentelium nigricans*) make diel movements between distinct locations of the stream (Matheney and Rabeni 1995). Similarly, in the Gila River, we observed suckers making daily foraging movements outside refuge habitats. Suckers consistently fed in habitats that were distant from daytime refuges, and Booth et al. (Chapter 1) observed that the abundance of *C. insignis* feeding scars in the Gila River was not related to distance to refuge habitats. Booth et al. (M. Booth, Chapter 3) also observed that *C. insignis* may use lower quality refuge habitats occasionally during low water but regularly during high water periods. Extended foraging trips into habitats distant from refuge sites may temporarily strand fish away from their preferred

habitats, causing them to utilize the closest available refuge site instead of returning to a home pool. Short-term displacements, whether intentional or accidental, potentially explain high daily turnover rates.

Although a small number of resident fish was consistently found within the focal pools, the overall population within the focal reach fluctuated over time as fish moved among habitats. Variation in population size over time may be problematic for assessing habitat quality based on population density, while movement parameters (e.g., immigration and loss) can be used to create metrics that provide more stable estimates of habitat quality (Bélanger and Rodriguez 2002). Some population fluctuations appeared to be related to increased movement during spates as well as electrofishing within the study reach, but many others had no apparent explanation. Small-scale and short-term movements may keep populations relatively fluid and distribute resource consumption over the stream as a whole (Chapter 1). In addition, fish activity quickly responded to spates, giving fish rapid access to newly inundated habitat with potentially novel resources. Turnover increased over time, leading to populations within the pools that substantially differed in the individuals present between the beginning and end of the monitoring period. Constant reshuffling of individuals within populations and consistent small-scale movements may allow fishes to recolonize habitats after disturbances and could serve to maintain genetic exchange within streams as a whole.

Although some Sonora suckers responded to spates, behaviors varied widely within the population, with individuals showing no response, temporary displacement to another location and subsequently returning to their home pool, or sustained displacement to an alternative habitat. Within-species variation in response to high flow events has been observed in other species of suckers (Jeffres et al. 2006), as well as galaxids (David and Closs 2002), while some fish show

no response to high flow events (e.g., hitch, *Lavinia exilicauda*; Jeffres et al. 2006). The way native species respond to floods is of particular importance in the western US, where controlled flood events have been used as management tools (Valdez et al. 2001, Jeffres et al. 2006) to reduce non-native species, assuming that native taxa are better adapted to resisting flood events (Meffe 1984, Schultz et al. 2003). Particularly in flood-prone or flow-regulated streams, accounting for variation in flow responses within and among species will be critical for managing fish populations.

Diel and small-scale movements can influence local population size and composition of individuals and species within habitats. Site fidelity and diel movements may potentially explain why large proportions of populations may appear sedentary (Rodríguez 2002) and indicate that the frequency of sampling efforts may change estimates of home ranges for many stream fishes. As tagging and tracking technology continue to advance, knowledge of variation in movement patterns among species and habitats as well as over long time frames will increase. Techniques like PIT telemetry enable detection of small-scale movements and provide individual information for entire populations of fish. As use of this technology becomes more widespread, it will be possible to test concepts and models of fish movement for a broad range of species and life stages at the generation scale.

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CHAPTER 3

Is mobility a fixed trait? Summer movement patterns of catostomids using PIT telemetry

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Abstract

Movement of fishes can control the structure of communities and populations, but for many common non-game taxa, relatively little information of this type exists. A growing body of information suggests that fish populations are composed of a mixture of sedentary and mobile individuals, but it is not clear whether movement behavior is plastic or fixed for individuals and what proportion of the population exhibits mobile behavior. To investigate the mobility and movement patterns of two common species of suckers, *Catostomus insignis* and *Catostomus clarki*, in the Gila River of western New Mexico, we tracked > 450 individuals over three summers using passive integrated transponder (PIT) telemetry. Both species were mobile and typical home ranges exceeded 300 m, but only about 25% of individuals were detected in a single habitat segment. We observed increased movement after spates caused by summer monsoon rains, and fish used areas of the stream differently under high and low flow conditions. Individuals predominantly used major refuge habitats, but during high flow periods, fish often used small refuge sites with more limited overhead cover. Fish moved farther between years than within years, but a subset of individuals was found in the same locations from year to year. Movement behavior does not appear to be a fixed trait for an individual, and many individuals exhibited both stationary and mobile behavior among years. Unlike salmonid populations, which often have a larger proportion of stationary than mobile fish, individual suckers appear to be predominantly mobile, suggesting that variation in movement behavior among freshwater fish species is substantial.

We also used our large movement database to estimate whether sample size biased estimates of movement parameters. We estimated that movement parameters would be

underestimated by 20-50% if we had tracked fewer individuals, but the degree to which parameters were biased varied from year to year.

Introduction

Movement of organisms at some scale is ubiquitous in all ecosystems and regulates not only the fate of individuals, but the structure and dynamics of ecosystems, communities, and populations (Nathan et al. 2008). For example, large-scale movements of fish can influence subsidies among ecosystems (Flecker et al. 2010) as well as recolonization following habitat alteration (Gowan and Fausch 1996). Understanding movement dynamics is especially important for managing fisheries because it regulates connectivity among populations, dispersal and colonization in new habitats, and interactions among species. Large-scale movements are often necessary for reproduction, avoiding adverse habitat or resource conditions, or dispersing (Bryant et al. 2009, Flecker et al. 2010, Young 2011).

Although there are notable exceptions (e.g., Matheney and Rabeni 1995, Skalski and Gilliam 2000, Crook 2004, Petty and Grossman 2004, Breen et al. 2009), the predominant focus of movement studies for freshwater fishes has been stream-dwelling salmonids (e.g., Gowan et al. 1994, Young 1999, 2011, Rodríguez 2002, Popoff and Neumann 2005, Gresswell and Hendricks 2007). Movement behavior may vary within and among species (Fraser et al. 2001, Rodríguez 2002) as well as within the same species among different environments (Woolnough et al. 2009) and life history stages (Young 2011) making generalization of movement patterns difficult, even within a single taxonomic group like salmonids. Given the inherent differences between salmonids and other freshwater fishes, the study of common, non-game fish taxa ubiquitous in

many stream ecosystems is needed for more complete understanding of fish movement dynamics (Petty and Grossman 2004, Breen et al. 2009).

Early studies of fish movement suggested that adult fish are relatively sedentary and often occupy limited home ranges over their lifetimes, but over the past half century, generality of this "restricted movement paradigm" (Gerking 1959) has been challenged by investigations with mixed results (Gowan et al. 1994, Rodríguez 2002) and alternative conceptual models have been proposed (Crook 2004). Advances in tracking technology like radio (Lucas and Baras 2000, Hodder et al. 2007) and passive integrated transponder (PIT) telemetry (Brännäs et al. 1994, Roussel et al. 2000, Zydlewski et al. 2001, 2006, Cucherousset et al. 2005, Hill et al. 2006, Teixeira and Cortes 2007), marking methods (Ficke and Myrick 2009), and study design (Albanese et al. 2003) have revealed that in many fish populations at least a portion of the individuals are mobile. This mobile-sedentary distinction is statistically consistent with leptokurtic movement distributions observed in many stream fishes (Skalski and Gilliam 2003), however, conclusions about movement distributions of fishes are generally based on data collected within a single season (reviewed in Rodríguez 2002) or small numbers of individuals. Although there is evidence that both individuals and populations may show substantial variation in movement patterns over time (Young 2011), advances in tracking technology can facilitate research on whether the proportion of mobile individuals changes depending on environmental conditions and if movement behavior is fixed or plastic for individuals (Rodríguez 2002).

In many streams (Lee et al. 1980) and particularly in much of the southwestern United States (Minckley 1973, Sublette et al. 1990), non-game species (e.g, catostomids and cyprinids) compose a substantial fraction, and often the dominant portion, of the fish community. There is limited knowledge of movement patterns for many common fish species in this region, and most

studies have focused on endangered taxa such as the razorback sucker in large rivers (Tyus and Karp 1990, Modde and Irving 1998, Mueller et al. 2000). Catostomids, which are often abundant in streams of the Southwest, offer a powerful opportunity to investigate how movement dynamics of how movement patterns vary within and among closely related species, understand the distribution of behaviors within a population, and assess the response of fishes to changes in environmental conditions. Data from these species are particularly valuable because rivers in the Southwest have experienced extensive human modification of temperature regime, flow, and sediment load, often with severe loss of habitat for native species (Rinne and Miller 2006). Movement provides important linkages among populations and habitats and understanding how native species move within this landscape is critical to define population size, the diversity of habitats in which the species occurs, and the vulnerability of a population to local versus regional disturbances.

A fundamental assumption of movement studies is that the behaviors of individuals selected for tracking are representative of the organisms and populations of interest. Most movement studies are limited by the numbers of fish tracked (e.g., radio telemetry) or the spatial and temporal resolution of the data collected (mark-recapture). Recent developments in passive integrated transponder (PIT) tag telemetry make it possible to track large numbers of animals over fairly broad spatial scales due to the low cost of tagging, although this technology is only effective in small-to-moderate-sized wadeable streams due to relatively small detection distances (up to about 1m; Roussel et al. 2000, Cucherousset et al. 2005, Hill et al. 2006, Zydlewski et al. 2006). While radio telemetry has advantages over PIT telemetry in terms of spatial scale and temporal resolution for individual fish (Lucas and Baras 2000), results based on limited numbers of fish may not be robust or representative of the movement patterns of the population as a whole.

We focus here on two species of concern (US Fish and Wildlife Service), the Sonora sucker (*Catostomus insignis*) and the desert sucker (*Catostomus [Pantosteus] clarki*). These species are locally abundant whose study can provide insight into variation in movement patterns within and among species. We collected movement data on 549 PIT-tagged fish over a 3-year period and detected most animals (>70%) multiple times. Our primary goal in this study was to describe movement patterns within and between the two species as well as among years. We also investigated whether movement behaviors are fixed for individuals. In addition we use sequentially larger portions of this data set to estimate the minimum number of individuals necessary to obtain reasonable estimates of movement parameters.

Materials and Methods

Study species

Members of the family Catostomidae (suckers) are often the most abundant large-bodied native fish in Southwestern streams. The Sonora sucker, *C. insignis,* and desert sucker, *C. clarki,* occur in a broad range of stream habitats, ranging from high elevation headwaters in the mountains of Arizona and New Mexico to lowland warm-water streams of the Sonoran Desert (Minckley 1973). *C. insignis* typically feeds on invertebrates and detritus (Schreiber and Minckley 1981, Pilger et al. 2010), and is abundant in deeper pools with restricted flow and fine substrates (Minckley 1973) where it is often found in large aggregations (>30 individuals, Chapter 2). *C. clarki* has cartilaginous edges on its jaws allowing it to scrape algae off the substrate (Minckley 1973, Minckley and Marsh 2009). For both species, limited foraging occurs during the day, with most activity occurring during low light periods (Chapter 2). In the West

Fork Gila River, adult individuals of both species typically take refuge in deep pools or beneath overhead structure during the day, and move into shallow water areas at night to feed (Chapter 2).

Study location

The upper Gila River is a tributary to the Colorado River that originates in the Mogollon Mountains of western New Mexico, and is one of the few remaining free-flowing rivers in the western United States. Our study site was located at the Heartbar Wildlife Area, NM, near the confluence of the West and Middle Forks of the Gila River, approximately 3 km downstream from Gila Cliff Dwellings National Monument. Flow in the Gila River is driven by snowmelt, and the region also experiences a summer monsoon season (July-September), which can account for a substantial proportion of the total annual rainfall (Sheppard et al. 2002). During May through July 2008 and 2009, we installed a gauge rod, and recorded water level at least once daily, and more often if there was a flood event. During June 2010, we recorded water level every five minutes using Hobo water level loggers (Onset Corp, Pocasset, MA) and developed a rating curve during the sampling period to estimate discharge (Gore 2007). Typical wetted width of the river during summer ranged from 7-14 m, but was variable within seasons due to spring runoff, summer dry periods, and monsoonal thunderstorms. Mean water temperature for May to July was 19 ± 3 °C (range 11-32) in 2008, 21 ± 4 °C (range 11 - 33°C) in 2009, and 19 ± 3 °C (range 13 - 26°C) in 2010. Estimated median river discharge during the same period was 0.63 m^3/s (range 0.24-4.54 m^3/s) in 2008, 0.23 m^3/s (range 0.11-8.84 m^3/s) in 2009, and 0.62 m^3/s (range 0.20-3.05 m^3/s) in 2010. The study reach is predominantly a riffle-pool structure with wide shallow runs and occasional beaver dams. There is a limited riparian forest of Fremont cottonwood (*Populous fremontii*) and Arizona sycamore (*Platanus wrightii*) and smaller shrubs.

Pool habitats are formed by large woody debris, undercut banks, canyon walls, or large boulders and contain depositional sediments (silt, sand, and gravel substrata).

Although both *C. insignis* and *C. clarki* were similarly abundant as juveniles, adult *C. clarki* were typically less abundant than *C. insignis* in the West Fork Gila (M. Booth, unpublished data; *C. insignis*: *C. clarki*; juveniles 0.9:1, adults 5.8:1). Native Gila trout *(Oncorhynchus gilae),* headwater chub *(Gila nigra),* longfin dace *(Agosia chrysogaster),* speckled dace *(Rhinichthys osculus),* and spikedace *(Meda fulgida),* as well as introduced species yellow bullhead *(Ameiurus natalis),* brown bullhead *(Ameiurus nebulosus),* green sunfish *(Lepomis cyanellus),* rainbow trout *(Oncorhynchus mykiss),* brown trout *(Salmo trutta),* smallmouth bass *(Micropterus dolomieu),* mosquitofish *(Gambusia affinis),* and red shiner *(Cyprinella lutrensis)* were also present, but substantially less abundant than the suckers (<10% of the fish biomass)..

We mapped the study reach using a GPS (Vista Cx, Garmin International, Olathe, KS) each season, characterized habitat type, substrate, width, depth and flow, presence of "refuge" features (e.g., woody debris, undercut banks) and created a GIS map using Manifold GIS 8.0 (Manifold Software Limited, Hong Kong). Because fish stayed in refuges during the day (when our surveys were performed) fish locations could be described as discrete habitat units (typically pools or debris piles) and we calculated all distance measures between the centers of these habitat units.

Tagging

The tagging reach studied was 1.8 km long, and flanked by an extended reach 1.3 km downstream and 1.0 km upstream used to detect movement outside of the tagging reach. In the

central tagging reach, fish were captured for tagging using electroshocking and hoop or fyke nets. An electroshocking survey of the entire reach was completed in early June each year as part of larger monitoring efforts at the site. Additional collection efforts were distributed throughout the remainder of the 2008 and 2009 seasons and focused on pool habitats suitable for hoop and fyke nets (Figure 3.1). Each fish captured was weighed (electronic balance or spring scale), measured (length to nearest mm), and tagged, and its capture location recorded. If a previously tagged fish was recaptured, we weighed and measured it to estimate growth. We tagged all adult and subadult *C. insignis* (260 ± 77 mm standard length (SL), *N*=430) and *C. clarki* (190 ± 41 mm SL, *N*=119) captured from 2008 to 2010 (May to July) (Table 3.1). Read-write half duplex PIT tags (134.2 kHz, 23 mm x 3.85 mm, RI-TRP-WEHP, Texas Instruments, Dallas, TX) were implanted in the body cavity of the fish using a scalpel to make a small incision just below the pectoral fin and a tag injector was used to inject the tag (MK-10 implanter, BioMark, Boise, ID). Injectors and scalpels were sterilized in 95% ethyl alcohol. The incision was coated with antiseptic liquid bandage (New Skin®). Each fish was released in the same location as it was captured or recaptured and observed until activity returned to normal. We held about 40 tagged fish in laboratory tanks for several weeks during summer 2008 and no fish lost tags in captivity. In the field, we only captured one *C. insignis* that had a scar from tagging but did not contain a tag. We did not observe any direct tagging mortality, and tagging efficacy for small-bodied fish appears to be high (Skov et al. 2005), with negligible effects on movement or survival.

We used a portable antenna system to scan habitats for tagged fish. Our portable unit consisted of a high performance low frequency backpack RFID reader/data-logger with slim antenna tuner board (Oregon RFID, Portland, OR) enclosed in a custom fabricated aluminum waterproof antenna housing with a 2.5 m fiberglass pole. Read range was approximately

Table 3.1**.** Standard lengths of fish tagged with passive integrated transponders (PIT) each year in the upper Gila River of western New Mexico, USA.

Tagging Year	*Catostomus insignis* Standard length (mm)			*Catostomus clarki* Standard Length (mm)		
	N	Mean ± SD	Range	N	Mean ± SD	Range
2008	233	268 ± 79	(100 - 415)	73	186 ± 43	(104 - 370)
2009	174	259 ± 76	(145 - 464)	37	194 ± 37	(150 - 292)
2010	24	211 ± 49	(152 - 310)	9	210 ± 41	(153 - 294)
Total	431	261 ± 77	(100 - 464)	119	190 ± 41	(104 - 370)

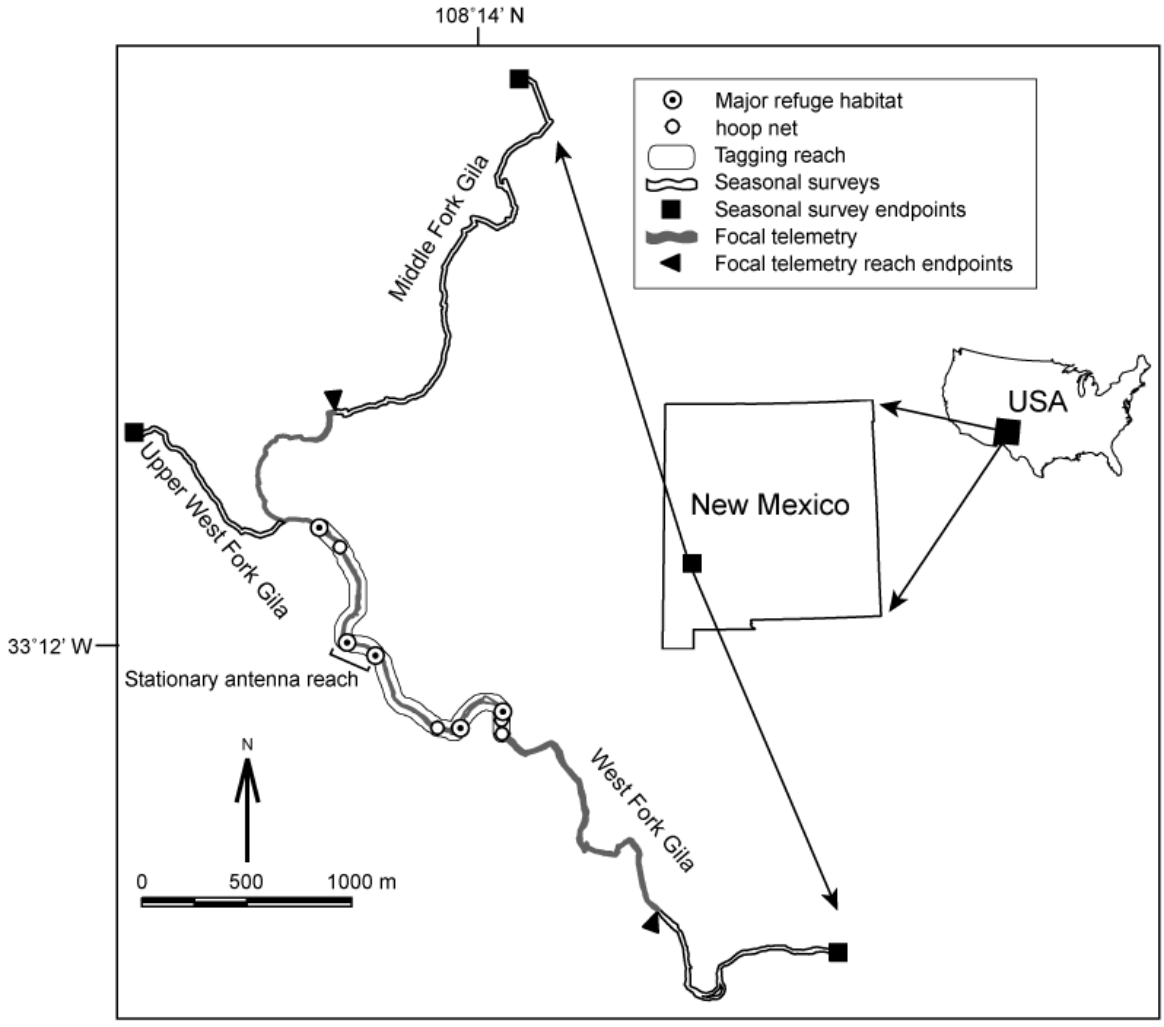

Figure 3.1. The upper Gila River of western New Mexico, USA. The tagging reach was downstream of the confluence of the Upper West Fork and Middle Fork of the Gila River. The grey-shaded section of stream bracketed by black triangles indicates the full reach regularly surveyed using portable PIT telemetry. Unshaded areas of stream indicate reaches that were sampled for tagged fish once each year via PIT telemetry or electroshocking. Locations where fish were captured via hoop nets, and major refuge habitats (also sampled using hoop nets) within the tagging reach, are indicated by circles. Eight stationary PIT antennas were installed in the central portion of the tagging reach during 2009 and 2010 (individual antenna locations not shown).

50-80 cm, depending on the orientation of the fish and the tag it contained. As tags were detected, tag information was displayed on a ruggedized palm computer (Meazura MEZ1000 Aceeca International, New Zealand) connected via a Bluetooth wireless serial adapter. We recorded the habitat location and detection time for each tag. In general, water clarity was sufficient to observe fish in water shallower than 0.5 m, so we restricted our search with the portable antenna to deeper water (>0.5 m) and all areas with overhead cover (e.g., roots, undercut banks) regardless of depth. For nearly all habitat scans, the antenna was submerged and placed as deeply beneath overhead cover as possible.

Once each season we tested our ability to detect tags in the field. Prior to a weekly survey, a colleague hid between 10 and 20 tags in locations that would normally be searched under the criteria listed above (in debris piles or deep water) and the survey proceeded as usual. The searcher did not have knowledge of the location of hidden tags. After the survey was complete, the number of hidden tags detected was tabulated and hidden tags were removed from the reach.

From 3 June to 4 August 2008, we collected fish position data within the 1.8 km tagging reach using the portable antenna system (N=9) and physical recaptures in nine pool habitats (N=9). From 18 May to 31 July 2009 (portable antenna N=12, physical recaptures N=7) and 2 June to 1 July 2010 (portable antenna N=5, physical recaptures N=4), our weekly sampling included the expanded reach 1.3 km downstream and 1 km upstream of the tagging reach (hereafter, “full reach”) to observe if animals had moved out of the tagging reach. A concurrent study in 2009 and 2010 (further described in Chapter 2) deployed a series of eight full-stream-width stationary PIT antennas installed in the center of the tagging reach (approximately 25 m apart), and continuously recorded small scale movement over a 200-300 m reach that included 1-2 large refuge habitats. In addition, once each in 2009 and 2010, we looked for fish outside of the

full reach; as part of the long term monitoring program of New Mexico Department of Game and Fish, we scanned physically captured fish (electroshocking) for PIT tags in a section 1.3 km downstream of the full reach, and used the portable antenna to scan an additional 1.3 km upstream of the full reach to look for fish that moved up the Middle Fork and West Fork of the Gila River.

For all surveys, we began at the downstream end of the reach and worked upstream. Under clear water conditions, surveys were completed within 5-8 hours, but more extensive search efforts when water was turbid took up to 10 hours. Sampling was less effective in turbid water because fish were not concentrated in refuge habitats, but were distributed throughout the stream (Chapter 2). The nature of search efforts (placing the antenna beneath overhead cover) typically disturbed fish within each habitat, but we rarely observed fish leaving the habitat being scanned during our searches. Because fish were typically disturbed by the presence of the portable antenna, we were able to determine if tags were still contained in live fish if the tag moved within the habitat. During surveys, we noted if a tag appeared to be dropped from a fish based on the following criteria: 1) a tag was detected multiple times in the same location within a habitat and did not move when area was gently disturbed, or 2) a tag was not detected in the concurrent study using stationary antennas despite remaining within the antenna reach during the entire season (i.e., the tag was stationary).

Movement analyses

To measure distances within our GIS map, we overlaid the wetted area of the stream with a 5 × 5 m grid of equally spaced points, and created a distance network of lines that connected grid points with the center points of fish habitat units. Using the built-in Manifold 8.0 function

"Select shortest path", we measured the minimum distance between points, constrained to paths within the wetted region of the stream.

For each individual and year with at least three observations, we calculated mean movement distance (mean linear displacement between successive detection locations) and home range (maximum linear displacement and total area used by the fish). Upstream movement was assigned positive values and downstream negative (hereafter, "signed movement"). Unsigned movements are the absolute value of the movement distances. Maximum linear displacement was measured as the distance between the two most distant detection locations within the individual fish's record, calculated as above. We calculated home range area using a linear buffer approach. Using all of the detection locations for an individual during each sampling season as well as in all years of the study, we buffered all movement paths and points in Manifold with a 25 m buffer width to create a polygon that included all detection locations as well as completely overlapping all of the wetted streambed. Because the stream channel varied in width, buffer polygons necessarily included substantial riparian habitat, which cannot be used by fish. To correct these home range estimations, we trimmed the buffer polygons using the wetted stream layer and discarded habitat outside of the wetted area of the stream. All detections of an individual fish (including physical recaptures) were included for the calculation of summary statistics, but when comparing movement rates ($m \cdot d^{-1}$), we only used data collected from portable telemetry surveys that incorporated the entire study reach to ensure that all segments of the study reach were represented.

We classified habitats as "major" if > 10 tagged individuals were typically observed in that location and "minor" if fish were rarely detected in the location or few individuals were detected in that habitat. Major habitats were primarily large deep (>1 m) pools with substantial

overhead cover (undercut banks, woody debris, overhead vegetation), while minor habitats had limited overhead cover and were typically shallow (<0.5 m), but still provided hiding places for fish.

We measured growth rates for all fish that were physically recaptured (*C. insignis N*=66, *C. clarki N*=3). To perform analyses comparing movement metrics to fish size, we estimated growth for fish that were not physically recaptured by fitting a modified Von Bertalanffy growth curve to yearly standard length (SL) growth data for those *C. insignis* we did capture (Fabens 1965) and used the growth model to estimate SL for fish (both species) that were not physically recaptured. If the last measured or estimated SL was greater than our calculated L_∞ (average maximum SL for the population), we used the last measured SL. For analysis, we binned fish into three size classes, based on natural breaks in the data and the fitted maximum size (*C. insignis*: <230 mm, 230 -350 mm, >350 mm; *C. clarki*: <170 mm, 170-230 mm, >230 mm). We did not have an adequate sample size to fit a Von Bertalanffy growth curve for *C. clarki*, therefore we used the *C. insignis* curve to estimate growth for C. clarki.

Determining the effect of sample size on movement parameters

Using our data set for *C. insignis*, we took a replicated subset approach to estimate how sample size influenced estimation of movement parameters. We created a custom script in JMP 8.0 (SAS Institute, Cary, NC) to iteratively create random replicated (*N*=1000) subsets of our overall data set for sample sizes ranging from 5 to 100 or 150 individuals depending on the year; the maximum subset size for each year was at least 20 individuals fewer than the number of individuals in the full data set. For each random subset, we found the maximum value of mean unsigned movement and maximum linear displacement. To assess the degree to which

movement parameters were underestimated for *C. insignis*, we compared the mean result of all replicates at a particular sample size to the value from the complete data set. We fit linear models of unsigned movement and maximum linear displacement to log-transformed sample size and used ANCOVA to assess differences in slope among years. Because our sample sizes for *C. clarki* were typically low, we projected the expected maximum value for larger sample sizes using the fitted logarithmic regression equation from *C. insignis* from the same year.

Results

Detection

Detection was high both for hidden tags and marked fish. Over the three years of this study, we typically detected 80-90% of the hidden tags. Of the 430 *C. insignis* and 119 *C. clarki* tagged, over the course of the study we detected 92% of *C. insignis* and 79% of *C. clarki* at least once, 75% of *C. insignis* and 50% of *C. clarki* three or more times, 63% of *C. insignis* and 29% of *C. clarki* five or more times and 31% of *C. insignis* and 8% of *C. clarki* on 10 or more occasions. We observed 27 shed tags (either from live or deceased fish) during the study (*C. insignis* 2008, N=8; 2009 N=12; 2010, N=3; *C. clarki* 2008, N=4, 2009, N=1, 2010, N=1).

Movement analyses

In 2008 and 2009, more than 75% of individuals of both species were observed in two or more locations within each year (range *C. insignis* 1-7, *C. clarki* 1-6). In 2010, 25% of *C. insignis* and 50% of *C. clarki* were observed in two or more habitats. Although there was a significant correlation between distance moved and the number of days-at-large (time between tagging and resighting) for 2008 (R^2=0.1, p<0.0001), 2009 (R^2=0.007, p=0.0004), and 2010 (R^2=0.03, p=0.002), none of the relationships had useful explanatory power. Yearly growth rates

(2009 and 2010 data pooled due to low sample size) ranged from 0-80 mm/year standard length and were strongly size dependent (R^2=0.73, $F_{1,64}$=176.91. p<0.0001,Von Bertalanffy coefficients L_∞ = 381, k=0.0007, Figure 3.2). We did not observe any measurable growth within summer seasons, suggesting that the majority of growth occurs during the rest of the year. If the annual growth we observed was evenly distributed throughout the year, summer growth rates should have been high enough to be within the detection ability of our methods.

Mean individual unsigned movement distance (absolute movement distance) for *C. insignis* was 205 m ± 19 (standard error) in 2008 (N=167), 141 ± 15 in 2009 (N=284), and 157 ± 27 in 2010 (N=120); for *C. clarki*, mean distance was 236 ± 41 in 2008 (N=37), 166 ± 39 in 2009 (N=43), and 347 ± 113 in 2010 (N=13). Overall, there was not an upstream or downstream bias in movement direction in any year or for either species (Table 3.2, Figure 3.3). However, there was a significant bias towards downstream movements ($p < 0.05$), often observed after major fish collection efforts within the study reach, on the descending limb of high flow events, and during minimum flow periods on some dates in 2008, 2009, and 2010 (Figure 3.4). Up to 24% of *C. insignis* and 15% of *C. clarki* individuals were detected only in their original tagging locations (Table 3.2), while up to 41% of *C. insignis* and 28% of *C. clarki* were observed in locations outside of their original tagging habitat segment, but returned prior to the end of the season. Many individuals were detected in the same habitat segment as their last known location during the previous year. *C. insignis* moved further between years than within years, (paired two-sided t-test 2008-2009 data: t_{131}=3.125, p = 0.002; 2009-2010 data: t_{110}=2.012, p=0.047) but *C. clarki* did not show this difference (Figure 3.5).

Table 3.2**.** Summary statistics for *C. insignis* and *C. clarki* with different movement behaviors within years: zero total movement, zero net movement, and all fish that moved (including net-zero movement individuals). Positive signed movements indicate upstream travel and negative movements are downstream. Unsigned movement is the absolute value of movement distance, regardless of direction.

	Zero movement[a]		Zero net movement[b]			Signed movement					Unsigned movement		
	N	% of total	N	Mean ± SE	Range	N	Mean ± SE	Median	Maximum downstream	Maximum upstream	Mean ± SE	Median	Range
2008													
Catostomus insignis	32	19%	56	64 ± 20	(0 - 760)	135	26 ± 19	0	-935	845	253 ± 22	182	(2 - 1199)
Catostomus clarki	3	8%	6	47 ± 36	(0 - 226)	34	33 ± 50	2	-731	785	257 ± 43	146	(8 - 905)
2009													
Catostomus insignis	68	24%	116	59 ± 11	(0 - 631)	216	4 ± 14	0	-1100	1453	186 ± 18	106	(2 - 2215)
Catostomus clarki	5	12%	12	29 ± 11	(0 - 112)	38	-64 ± 49	-23	-752	1310	188 ± 43	70	(10 - 1310)
2010													
Catostomus insignis	28	23%	45	58 ± 25	(0 - 1079)	92	-7 ± 27	0	-879	1073	206 ± 34	83	(11 - 1799)
Catostomus clarki	2	15%	2	0	-	11	-2 ± 90	22	-472	706	411 ± 125	296	(42 - 1328)

Note: Statistics only include fish observed at least twice after release. Movements are incremental distances between subsequent detection locations.

[a] Fish that were not observed to move from their tagging location

[b] Subset of fish that moved, but returned to their original location. These individuals are also included in signed and unsigned movement statistics

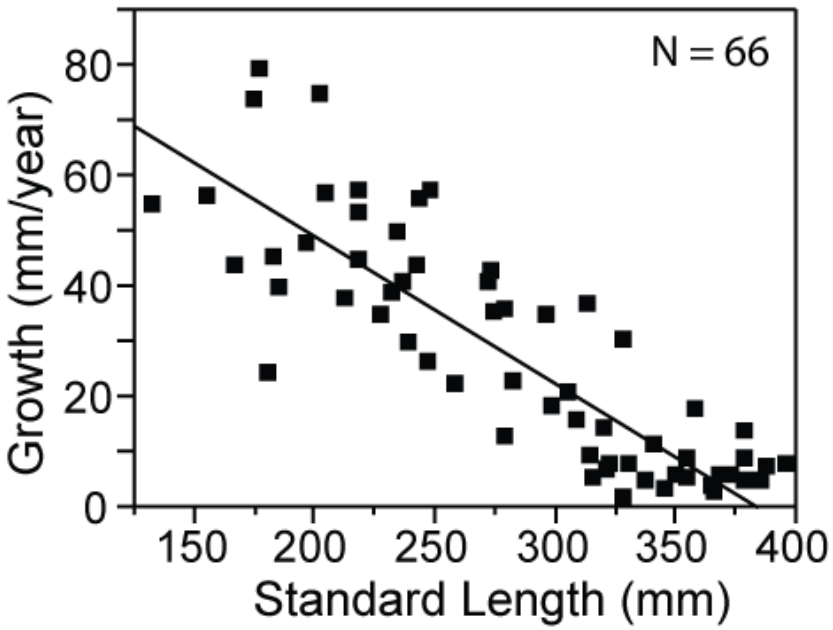

Figure 3.2. Yearly growth rates as a function of body size (initial standard length) for *C. insignis*. Growth rate = -0.266×SL – 102.234 . Von Bertalannfy growth parameters: L_∞ = 381, k=0.0007. We did not have sufficient sample size (N=3) for a growth analysis of *C. clarki*.

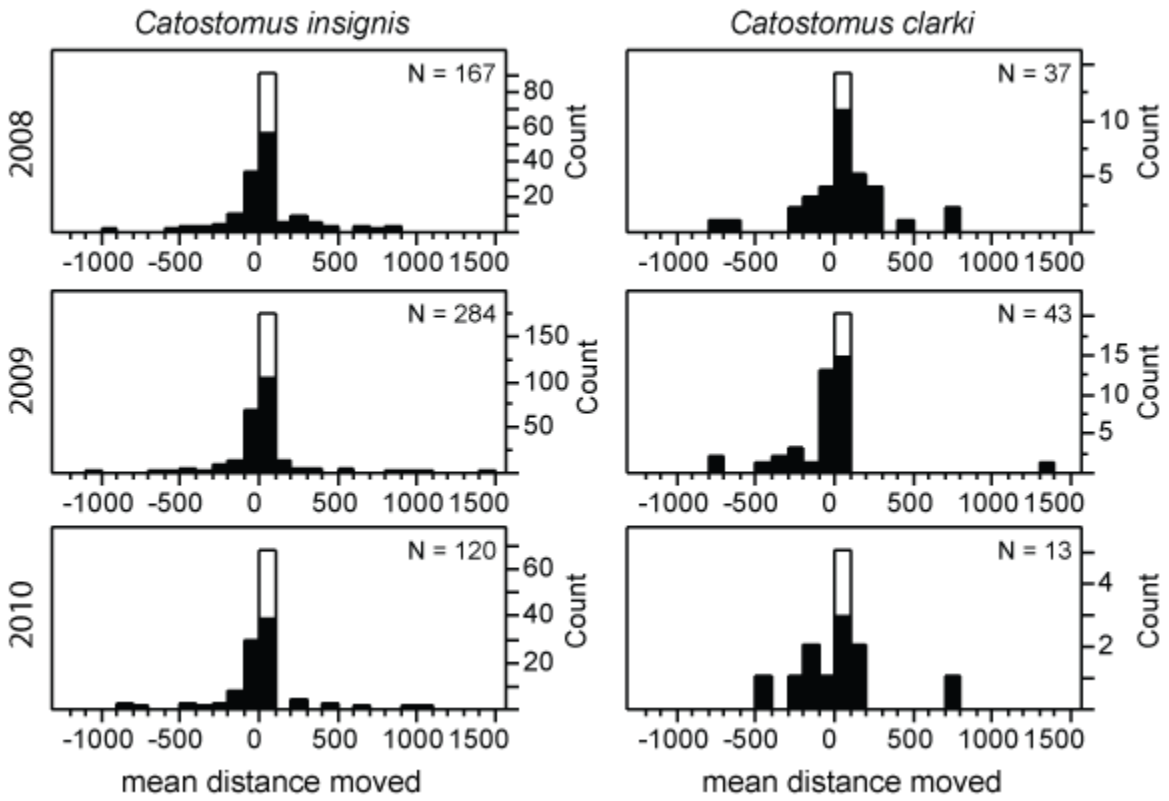

Figure 3.3. Mean movement upstream (m) (positive values) or downstream (negative) for *C. insignis* and *C. clarki*. Black bars indicate individuals that were detected outside of their initial tagging location, white bars indicate individuals detected only within a single habitat. Data shown only for individuals detected at least twice during the sampling period. Note that count axis differs among panels.

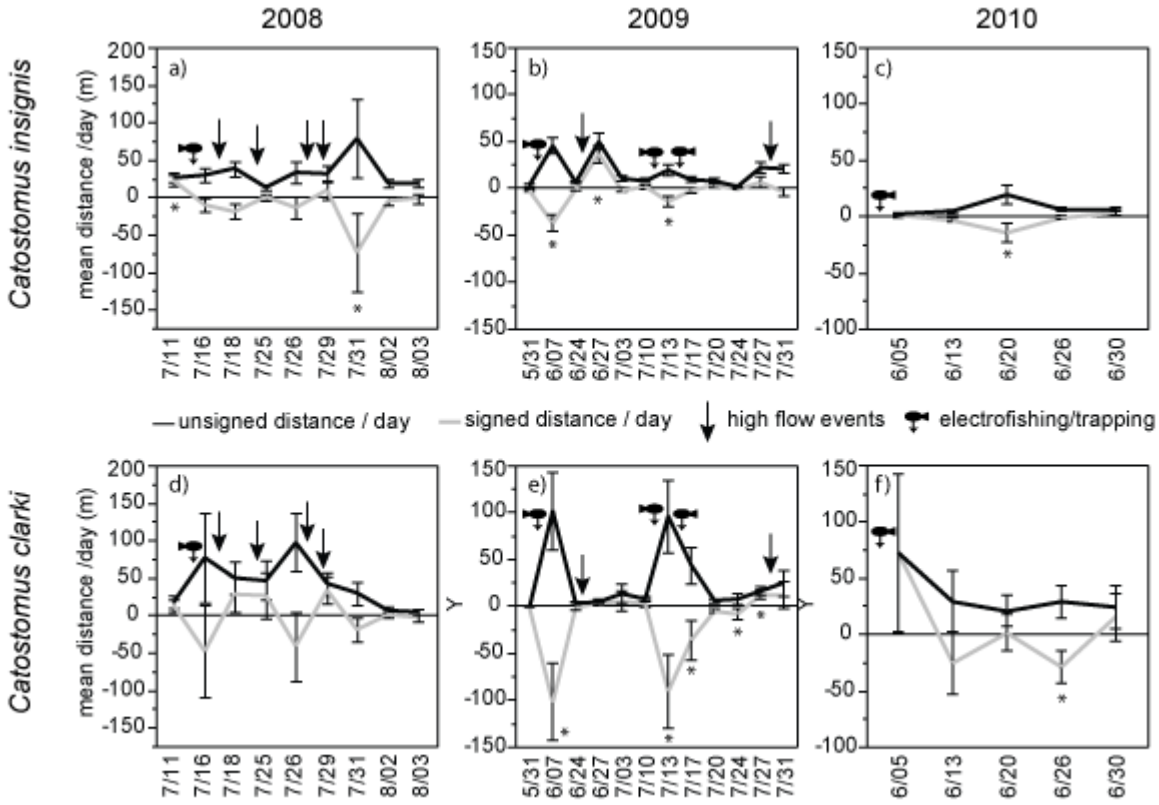

Figure 3.4. Movement rates (m/day; signed and unsigned) observed during each telemetry survey. Unsigned movement distance is the absolute value of distance moved, regardless of direction, and signed movement is the distance moved up- (positive values) or down- (negative values) stream. Arrows indicate high flow events and "fish" indicates fish sampling efforts within the reach. Asterisks indicate dates when the average movement rate was significantly different from zero (net directionality upstream or downstream). Note that dates are not evenly spaced.

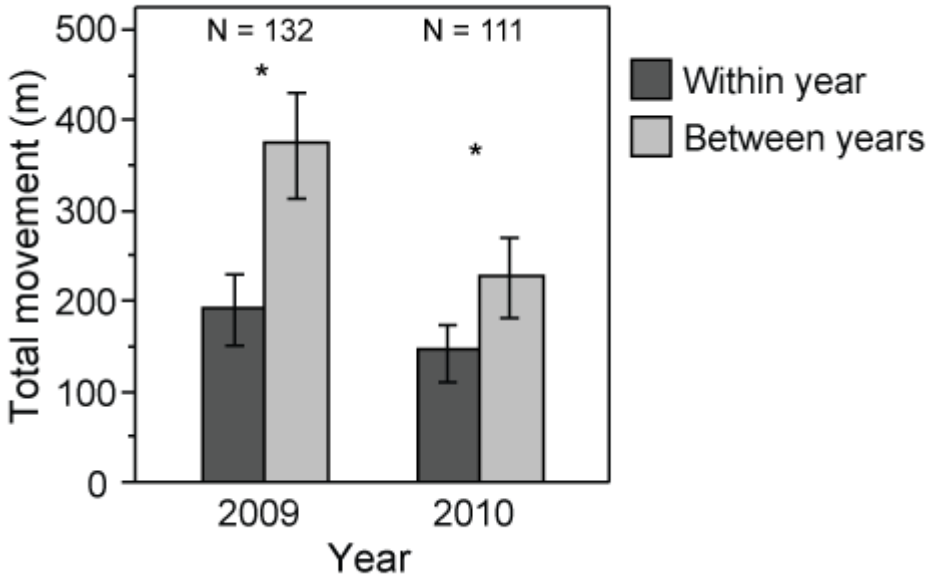

Figure 3.5. Observed movements within a summer compared to movements between years for *C. insignis*. Within year movements were calculated as the absolute value of the sum of all signed movements for an individual within a year, between year movements were the distance between the last observed location in the previous year and the first observation in the year indicated on the graph (2009: movement between 2008 and 2009; 2010: movement between 2009 and 2010). Asterisks indicate significant differences ($p<0.05$) between within-year and between-year movements.

Mean maximum linear displacement ranged from 310 to 479 m for *C. insignis* and 511 to 692 m for *C. clarki* among years of the study (Table 3.3, Figure 3.6). Maximum linear displacement was smaller for *C. insignis* in 2010 than in 2008 or 2009 (Tukey-Kramer HSD q*=2.350, 2008-2010: p=0.039, 2009-2010: p=0.023). Home range (Table 3.3) followed a similar pattern, with smaller home ranges in 2010 than in 2009, but no difference between 2008 and either year (Tukey-Kramer HSD q*=2.34987, 2008-2009: p=0.8199, 2008-2010: p=0.1606, 2009-2010: p=0.0297). *C. clarki* did not show any differences in maximum linear displacement or home range among the years of our study. The reduction in home range in 2010 may be an artifact of the more limited sampling effort, but 2010 lacked flood events during the sampling period and fish potentially experienced higher energetic costs associated with high spring discharge which may also have reduced the extent of fish movements.

We classified individuals as "non-movers" if they were only detected in a single location during a season, and "movers" if they were observed in at least 2 locations during a season. Individuals did not appear to be distinct stationary or mobile "morphotypes". However, 57% (N=97) of *C. insignis* were classified as movers in all years they were detected, 9% (N=15) were consistently non-movers, and 34% (N=58) exhibited both behaviors over the course of our study. Initial fish size influenced the consistency of behavior (Likelihood ratio χ^2=10.101 p=0.0388) with more large fish consistently exhibiting mobile behavior. More small fish (<230 mm SL) exhibited both behaviors than larger fish, however, there was not a consistent shift in behavior as fish grew. No large fish (>350 mm SL) were consistently non-movers. For *C. clarki*, 76% (N=13) were always movers, 6% (N=1) were consistently non-movers, and 18% (N=3) were classified as both. We did not have sufficient numbers of *C. clarki* to test the influence of size on movement behavior.

Table 3.3**.** Mean movement distance, maximum linear displacement, and home range area for tagged *C. insignis* and *C. clarki* observed two or more times per year in the Gila River. Values are means ± (s.e.)

	Catostomus insignis			*Catostomus clarki*		
	2008 (N=167)	2009 (N=284)	2010 (N=120)	2008 (N= 37)	2009 (N=43)	2010 (N=13)
Mean movement distance (m)	205 (19)	141 (15)	158 (28)	236 (41)	166 (39)	348 (113)
Maximum linear displacement (m)	479 (39)	476 (38)	310 (47)	615 (90)	511 (105)	692 (185)
Home range area (m^2)	6685 (514)	7164 (551)	4893 (664)	8511 (1138)	8661 (1775)	10530 (2764)

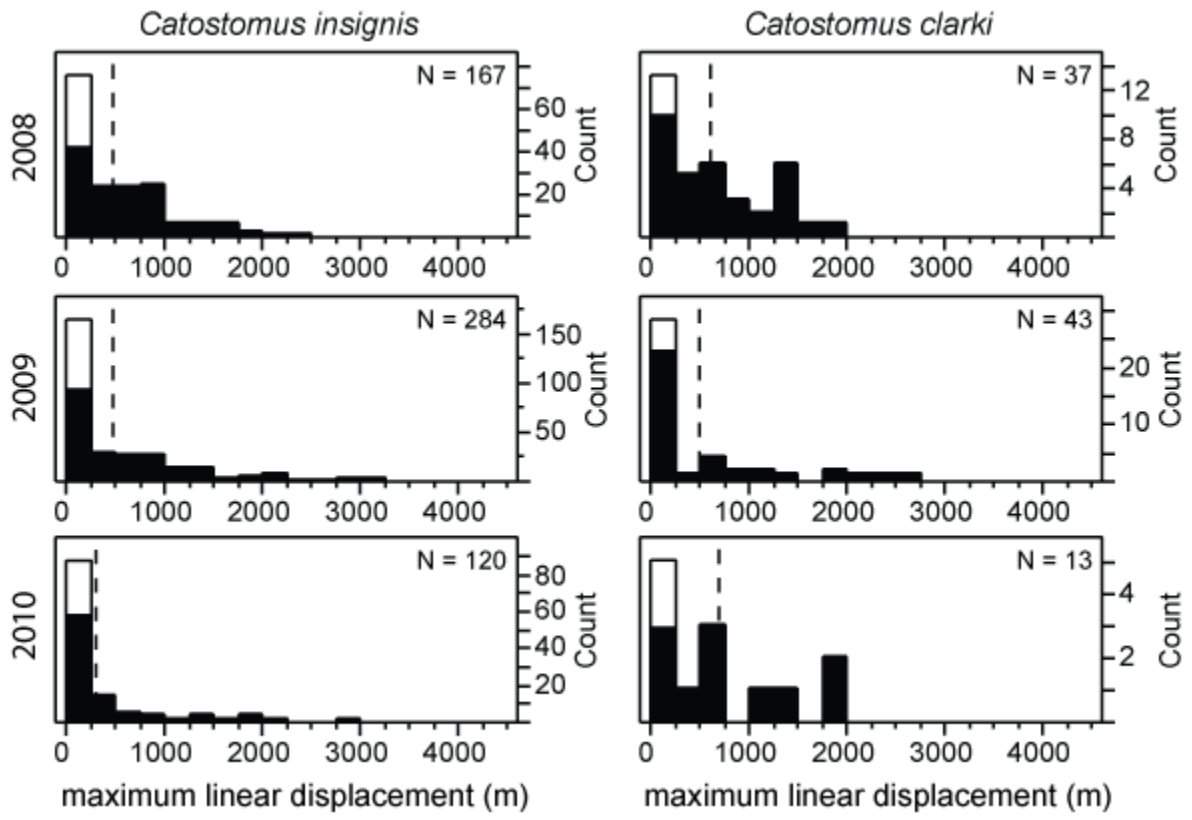

Figure 3.6. Maximum linear displacement (home range) for *C. insignis* and *C. clarki*. Black bars indicate individuals that were detected outside of their initial tagging location, white bars indicate individuals detected only within a single habitat. Data shown only for individuals detected at least twice during the sampling period. Note that count axis differs among panels.

Although some fish were classified as "zero movement" fish (individuals detected at a single location only; Table 3.2), the concurrent effort with stationary antennas in 2009 and 2010 showed that even those fish made regular sojourns outside of the pool where they were detected via portable telemetry. The durations of these movements were shorter than the separation between subsequent portable telemetry surveys (hours to days). In 2009 and 2010, we observed 31 and 21 "zero-movement" *C. insignis*, and one and two *C. clarki*, to have undertaken movements of at least 25 m outside the habitat where they were observed via portable telemetry.

The proportions of observed movements between major and minor habitats were different among the years for *C. insignis* (χ^2=111.1 df=6, p<0.0001), but not for *C. clarki* (χ^2=6.08 df=6 p=0.414). In 2010, the majority of *C. insignis* movements were among or into minor habitats and indicated greater use of minor habitats than in previous years (Figure 3.7). Periods of higher flow typically increased the proportion of fish observed in minor habitats, although *C. clarki* also was predominantly found in minor habitats immediately following the major electroshocking surveys in early June 2009 and 2010 (Figure 3.8).

There was one substantial flood in the 2009 season (discharge increased from baseflow of about 0.4 m^3/s to greater than 5 m^3/s within 10-20 minutes). We conducted a similar number of telemetry surveys before and after the flood. We observed 204 *C. insignis* and 18 *C. clarki* prior to the flood event and 238 and 22 after the flood, respectively. Of the fish observed post-flood, 44 *C. insignis* and 4 *C. clarki* had not been detected in the reach prior to the flood during 2009. Ten *C. insignis* were observed prior to the flood, but not observed again within the reach during 2009. Only one of the fish that left after the flood was seen in the 2010 season.

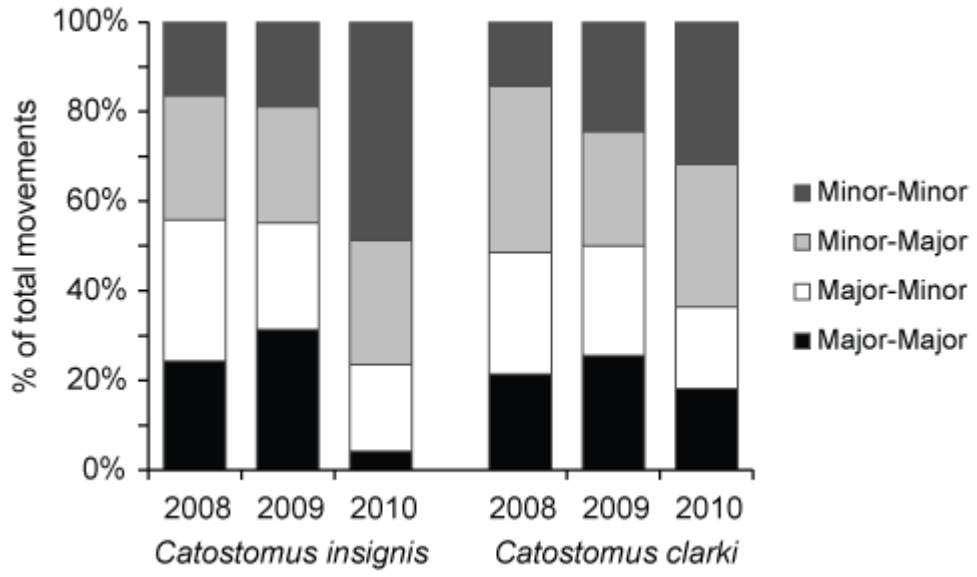

Figure 3.7. Proportion of total movements among habitat types for *C. insignis*. The first label indicates the habitat type departed from and the second label the habitat type moved into (i.e., Minor-Major indicates a movement from a Minor into a Major habitat). Major habitats were locations with refuge habitat (e.g., deep water, overhead structure) with consistently high tagged fish abundance (>10 individuals). Minor habitats were had limited refuge structures and typically contained few fish.

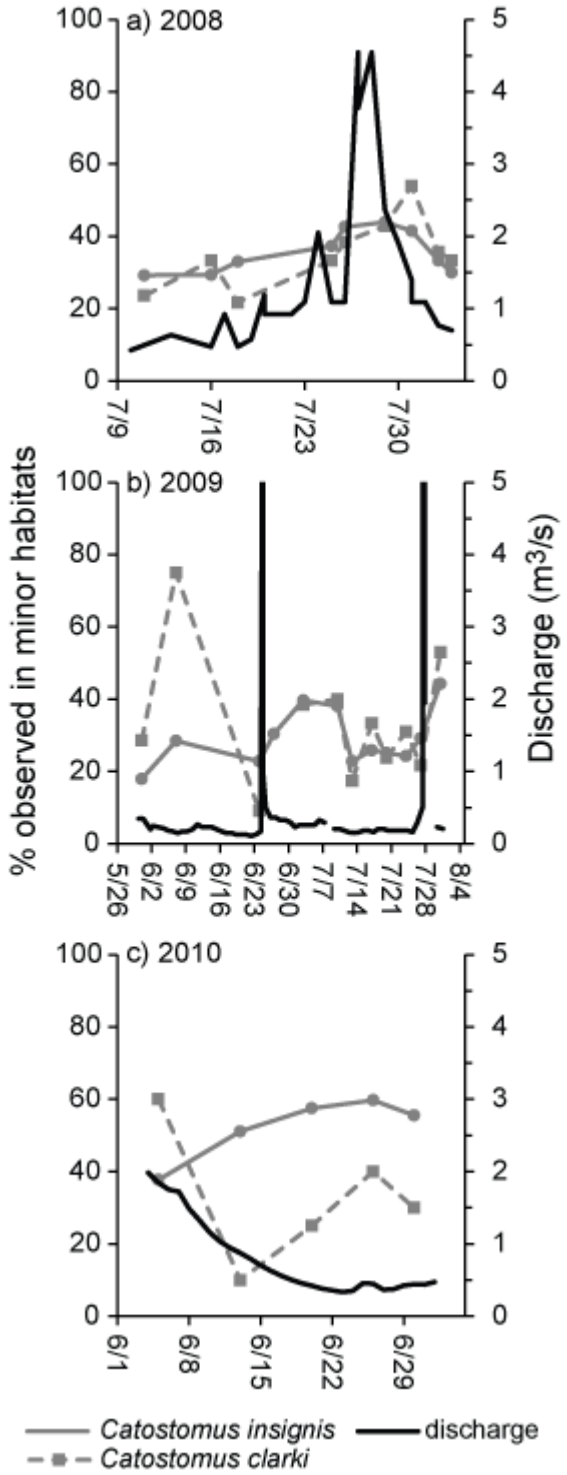

Figure 3.8. The relationship between the proportion of fish observed in minor habitats and stream discharge.

Although we sampled a broad range of sizes (Table 3.1) of both species, we did not observe any correlation of standard length to any movement metric (mean movement distance, home range, maximum linear displacement, directional bias). We also did not observe any correlation of growth rate or body condition (Fulton's condition factor; Bolger and Connolly 1989) with our movement metrics.

Effect of sample size on movement parameters

For Sonora suckers, we found that the mean maximum distance for subsets of movement records with a sample size of 150 represented 97-98% (2008 and 2009) and a subset size of 100 represented 96% (2010) of the known maximum distance for the complete data set. We observed rapid increase in the population maximum value for linear displacement and mean distance as increasingly larger subsets of data for individuals were included in the analysis up to subsets containing 75 to 100 individuals, beyond which estimates approached the values observed in the complete data set (Figure 3.9). A small survey of recent radio telemetry studies (N=15, Appendix 1) suggests that the typical number of individuals tracked is about 20 (range 3-43). Using a subset size of 20 individuals in our analyses, maximum linear displacement is underestimated by 28 to 35% and maximum mean distance by 28 to 62% compared with values obtained from the complete data set for each year. The slope of accumulation curves (Figure 3.9) differed significantly among years (maximum linear displacement: Log sample size ANCOVA $F_{5,26994}=7592.27$, $p<0.00001$, maximum mean distance: $F_{5,2699}=5709.15$, $p<0.00001$), and was greater in 2009 and 2010 than 2008. In other words, fewer fish were needed in 2008 to describe the range of these movement parameters than in 2009 or 2010.

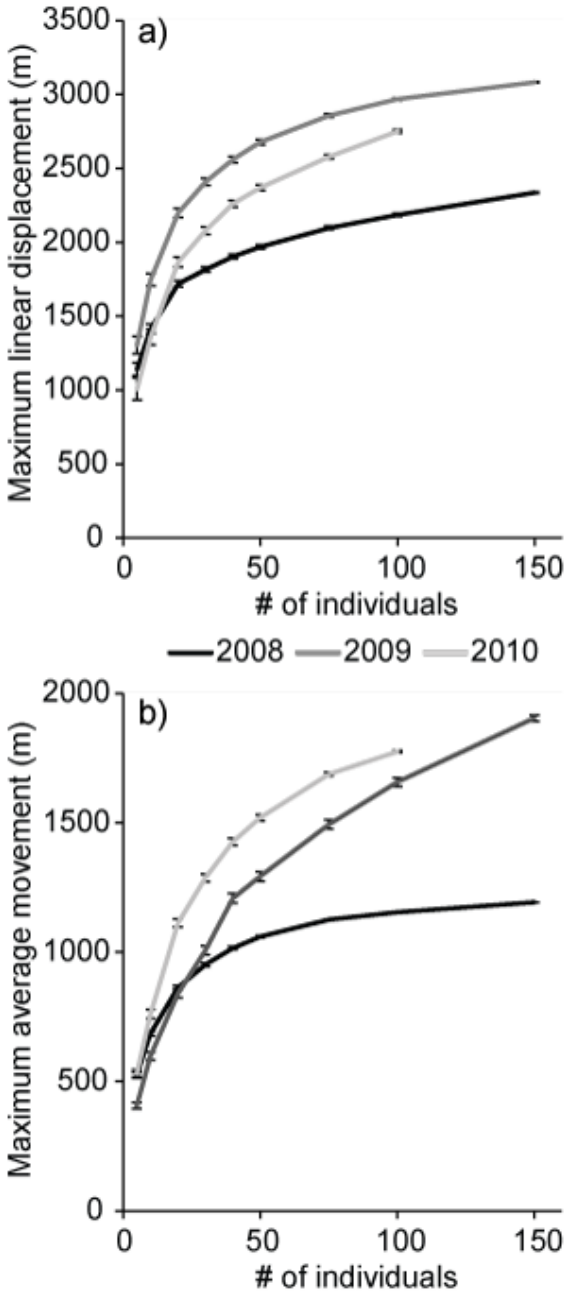

Figure 3.9. Mean of a) maximum linear displacement (± s.e.) and b) maximum average movement (± s.e.) of *C. insignis* estimated using subsets of sample data of increasing size for each study year. Standard errors are small relative to the axis scale and are masked by the thickness of the trendline. Data represents 1000 random draws of individuals from the total pool per subset size.

Discussion

The patterns of movement by two ecologically significant species of catastomid fish, native to streams in the southwestern US, varied markedly in the Gila River, NM, from year to year as well as among individuals. Although we have less robust data for *C. clarki*, for both species we observed a relatively high proportion of individuals that exhibited both mobile and sedentary behaviors for extended periods, providing evidence that movement behavior is not fixed for an individual, even within the same life stage. Individuals varied substantially within each species, but unlike much of the salmonid literature (Rodríguez 2002), we found that mobile individuals made up a large proportion of the population. We expected that individual movement might respond coherently to changes in the abiotic environment (e.g., floods; Harvey et al. 1999) as well as attributes of the fish (e.g., size; Schrank and Rahel 2006). Abiotic environmental conditions did not appear to influence movement patterns in a consistent way. Although stream discharge differed markedly among years (2008 and 2010 were wet winters with higher snowpack and discharge, while 2009 had minimal winter precipitation and low baseflow), year-to-year behavioral shifts from high-flow to low-flow conditions were not consistent among individuals. We did not observe any consistent expansion or reduction of home range among individuals with variation in environmental conditions, suggesting that other factors may play a larger role in determining the extent of individual movement.

The majority of the individuals sampled made relatively large movements within the summer season, as well as from one summer to the next. Proportionally more *C. insignis* than *C. clarki* were non-movers found repeatedly (exclusively or nearly exclusively) in a single location (consistent with other work with these species; Booth and Shipley, in press). But in general, *C. insignis* and *C. clarki* did not differ significantly in their movement parameters, although

previous accounts (Minckley and Marsh 2009) describe these species as having different food and habitat preferences (see Methods). Other studies have shown that fishes with differing diets and microhabitat preferences tend to have different movement dynamics (e.g., brown trout, white sucker; Brown et al. 2001; hitch and Sacramento sucker; Jeffres et al. 2006). In contrast to those other species, our observations suggest that in the Gila River these two species may not differ in microhabitat preferences (adults of both species regularly co-occurred in most habitats) compared to other streams in the Southwest. The degree to which *C. insignis* and *C. clarki* diets overlap (ranging from invertivore and herbivore, respectively, to facultative omnivores) appears to be variable among streams and seasons (Schreiber and Minckley 1981, Clarkson and Minckley 1988, Pilger et al. 2010), and diet overlap observed in the Gila River (Pilger et al. 2010) partially may be a result of similar movement behavior. Understanding how diet and phylogeny exhibit strong control over fish movement patterns is necessary to understand variation within and among species and will determine the extent to which movement behavior can be generalized.

The nature of our study design did not enable us to compare short-term movement patterns of the two species. We tracked fish during the day when they were hiding in refuge sites rather than during their evening foraging movements because it was not possible to approach fish close enough to detect their tags while they were foraging. Therefore, in this study we documented sustained displacements among habitats over a large spatial scale (>1 km), while concurrent data collected using stationary antennas indicated that the majority of fish performed nightly foraging movements from focal refuge sites into adjacent shallow habitats (at least 25 to 200 m away). Nightly foraging trips are likely to be leptokurtically distributed, with the majority of trips occurring relatively close to the refuge habitat due to variation in exploratory behavior

among individuals (Fraser et al. 2001). Short-term forays, like the overnight trips observed in *C. insignis* and *C. clarki,* may give fish information on the distribution of resources within the stream and thereby determine the amount of habitat that an individual requires to feed, grow, and reproduce. The actual sizes of home ranges was likely even larger than our data indicate because we were only able to survey the full reach about once each week, and so may have missed displacements at shorter time scales of 1-6 days (Baras 1998, Ovidio et al. 2000). Despite these limitations, we observed movement by both species and summer home ranges on the order of kilometers, and we expect that these estimates are robust minimum estimates of fish movements in the Gila River.

Although we expected that changes in discharge might modify the direction or magnitude of movements, neither species consistently moved up- or downstream following flood events. High flow events in 2008 resulted in net downstream movement, while those of similar magnitude in 2009 resulted in upstream displacement. This outcome may have been due to fish using sheltered refuge habitats during high flows (Harvey et al. 1999) or to fish being capable of orienting to high flows to avoid displacement (Meffe 1984). Previous work indicates that the fishes of the Southwest, including *C. insignis* and *C. clarki*, exhibit behaviors that limit displacement by flood events (Meffe 1984, Rinne and Stefferud 1997, Schultz et al. 2003, Booth and Shipley in press). The behavioral response of fishes to high flow events and their ability to resist displacement will determine how fish communities are structured over short time periods (Matthews 1986). For example, major flooding appears to limit the colonization and persistence of non-native fishes in the southwestern US, while stabilization of flow regimes allows non-natives to proliferate, to the detriment of native fauna (Schultz et al. 2003).

Elevated flows, potentially interacting with turbidity levels, increased the proportion of fish using minor (i.e., small, marginal quality) refuge habitats. Minor habitats typically did not provide ample overhead cover or were extremely shallow during low flow periods. Few individual fish were consistently found in the same minor habitat, indicating that those areas were potentially marginal habitat for refuge and used only transiently. However, in 2010 (a high discharge year), the majority of *C. insignis* movements were into minor habitats. While major refuge sites may provide high quality refuge habitat for large numbers of individuals, use of minor refuges may be advantageous if they give closer access to less frequently available feeding habitats at the cost of potentially higher predation risk. In high flow periods, minor habitats may provide sufficient refuge due to decreased visibility from increased water depth and elevated turbidity, but in low flow periods they are likely too risky for consistent use by individuals. Many species of fish show strong associations with discrete habitat patches (Fausch et al. 2002, Belica and Rahel 2008) and conceptual models (Schlosser and Angermeier 1995) show that the typical life cycle of a stream fish consists of movements between refugia and favorable feeding habitats. Variation in refuge quality, both among sites and within a site over time, will likely play an important role in determining the distribution of fishes and the movement of fishes among habitats. For example, increasing the complexity of habitat, while controlling for habitat size, greatly increases diversity of fish species found in artificial habitat patches in a tropical river (Arrington et al. 2005)

Interestingly, flood responses by the fish were of a similar magnitude to movements coinciding with our collection activities, although sampling-induced movements were typically downstream, while movements immediately following flooding generally had little or no net direction. Unlike studies involving salmonids which have indicated either little movement

(Young and Schmetterling 2004) or upstream movement (Peterson et al. 2005), we observed downstream movement following fish collecting activities. We suspect some of the downstream movements were a return of individuals to their prior habitat—electroshocking efforts downstream appeared to "herd" fish upstream into major habitats, while hoop and fyke nets may have captured visiting individuals during nightly foraging forays. Electroshocking in downstream habitats in 2009 elevated population sizes in upstream habitats (Chapter 2), which then dropped to pre-electroshocking levels within a few days as fish returned downstream. Electroshocking occurred only once per season during our study and likely did not modify movement over the entire season. However, given that many mark-recapture studies rely on electroshocking to capture fish and estimate movement parameters, it is critical to know whether individuals respond to sampling efforts, on what time frames, and if other taxa show different responses.

In all years of the study, mean movement distance by suckers in the Gila River was on the order of hundreds of meters, although some individuals of both species were observed to make distinct movements of over a kilometer and overall displacements of several kilometers. Home ranges were typically several hundred meters long (measured as maximum linear displacement) and included several distinct refuge habitats. There is evidence that habitat size may drive the overall range of fish movement (Woolnough et al. 2009), and we observed higher movement distances by *C. insignis* and *C. clarki* than did Booth and Shipley (in press) for the same species in streams in Arizona, likely in part because the Gila River and the spatial scale of the study reported here was larger than the small streams (6 km vs hundreds of m; median discharge <0.1 m^3/s) studied by Booth and Shipley (in press). The movements detected in this study are similar in magnitude to those observed by Siebert (1980) and Williams (1991) for

C. clarki. Unlike Siebert (1980), who found that suckers exhibited a tendency to move into a canyon-bounded reach of Aravaipa Creek during summer, we did not observe directional movements upstream into the canyon-bounded reach of the Middle Fork of the Gila River. Other species of suckers in larger rivers are highly mobile during non-reproductive periods (Chart et al. 1992, Matheney and Rabeni 1995) and it seems likely that mobility may be a characteristic of catostomids in general.

Unlike other studies that have found that movement patterns were related to fish length (Trinidad killifish; Fraser et al. 2001; cutthroat trout; Gresswell and Hendricks 2007) and growth (Kahler et al. 2001, Steingrímsson and Grant 2003), we did not observe any relationship between size or growth and any movement parameters. Young (2011) found that rapidly growing cutthroat trout were somewhat more likely to move and large mobile individuals tended to move farthest, but did not see a link between size and probability of movement. He attributed the disconnect of size and movement to displacement of large, dominant individuals triggering cascading movements among smaller, less competitive individuals, eventually causing individuals of all size classes to move. Suckers do not appear to compete directly for space, in that they do not hold defined feeding stations, are often dense in refuge habitats, and they have regularly been observed feeding in groups of two or more (M. Booth, pers. obs.). We have not observed any antagonistic behavior among individuals. In addition, all of the individuals tracked in this study were adult fish; it is possible that sub-adult and juvenile fish display different movement dynamics which may be size or age related. In the current study, many movements may simply have been the result of fish entering the nearest refuge site after a nighttime foraging trip, and may explain the overall lack of directionality detected in their movements.

In contrast to our findings, previous work on the Gila River by Bestgen et al. (1987). suggested that *C. insignis* and *C. clarki* are not mobile. However, the minimum movement distance that could be detected in that study was 1 km due to the non-contiguous nature and length of the study reaches, making the small- to moderate-scale movements (20 m to 2 km) we documented difficult or impossible to detect. In addition, sampling by electroshocking in the upper Gila is relatively inefficient due to the presence of deep pools where fish are out of range of the gear (M. Booth, unpublished data), and this likely contributed to the low recapture rates (2-4%) in the study by Bestgen et al. (1987). Low recapture rates have been implicated in underestimating the mobility of fish (Gowan et al. 1994); the high efficiency of portable telemetry made possible the recapture rates (> 75%) we experienced.

Although we collected movement data over several years, we only collected data during summers, meaning that we have measures within summers and can compare locations of fish from one summer to the next, but have no information for other times of year. While we observed movements within and among years, it is possible that Sonora and Desert suckers also make major spawning movements in spring, when discharge was too large to deploy our telemetry equipment. Related catostomid species are known to perform spawning migrations (Tyus and Karp 1990, Decker and Erman 1992, Modde and Irving 1998, Schmetterling and Mcfee 2006, Compton et al. 2008, Sweet and Hubert 2010) and historical, anecdotal reports from Arizona (Minckley 1973) suggest that the major rivers of the Southwest have experienced large spawning runs of fish, at least in the past. Given that these species are of conservation interest, it will be particularly critical to understand if these fish make spawning migrations, which would provide a genetic link between up- and downstream populations and enable recolonization of habitats after local extirpation. We observed high fidelity of some individuals to our study reach

among years (Booth, Chapter 2), suggesting that if spawning movements occur, individuals exhibit some level of homing behavior to their summer habitat. Homing behavior has been observed in other benthic fishes in large rivers, although individuals varied in motivation or ability to return to a focal habitat (Crook 2004). The prevalence of homing behavior may vary with environmental conditions, food availability, or behavioral interactions, and similar to plasticity in movement behavior, individuals may change homing behavior depending on the context.

Subset analysis

Other studies have considered the effects of the timing of sampling surveys (Baras 1998, Ovidio et al. 2000) and number of detections per individual (Crook 2004) on the estimation of home ranges. However, it remains unclear how estimates of movement parameters at the population level vary based on the number of individuals tracked – probably because there are relatively few data sets containing sufficiently large numbers of fish that were tagged and subsequently detected multiple times. PIT telemetry (e.g., Cucherousset et al. 2005, Bubb et al. 2006, Hill et al. 2006, Teixeira and Cortes 2007, Enders et al. 2007, Johnston et al. 2009) shows great promise for in-depth, long term studies investigating variation in movement parameters within populations and through time. We found that the number of individuals included in movement estimates can strongly influence the estimation of population-level parameters, particularly if there is marked variation in behavior among the individuals. Although radio telemetry has important advantages over other approaches because of its ability to detect long distance movements as well as to provide high resolution temporal data (Lucas and Baras 2000), our analysis suggests that the number of individuals typically used in radio telemetry studies (3 – 49; Appendix 1) would almost certainly have led to significant underestimates of both home

range and average maximum movement despite the fact that there is likely an asymptotic relationship between sample size and parameter estimates (Crook 2004). We estimate that a sample size of 75-100 individuals would be required to assure that the full range of individual movement distances we observed in our full data set of 431 fish is adequately represented. This required sample size will no doubt vary depending upon taxon, site, and environmental conditions, and the degree of variation in movement behavior within taxa will determine the effect of sample size on estimate quality. Based on our subset analysis using our extensive *C. insignis* data set, it is likely that we have underestimated movement parameters for *C. clarki* because our data are much more limited (the species was relatively rare in our study area). This observation suggests that *C. clarki* may be more mobile than the estimates we report here imply. If we assume that the relationships between sample size and parameter estimates are similar for *C. clarki* and *C. insignis* within years, maximum linear displacement for *C. clarki* was likely underestimated by 20 to 40% (about 375-800 m) and average maximum movement by 19-49% (about 170-640 m). Underestimates of movement parameters may be particularly problematic when they are used to infer fish production, the size of habitats necessary to maintain populations, the degree of connectivity among populations (Gowan et al. 1994), and the effects of ecosystem engineering behavior (Chapter 1).

Continued advances in PIT telemetry, as well as other technological innovations in tracking methodology, will make data collection on the population scale more feasible and provide significant advantages in assessing population-level movement and demographic analyses. Our data indicate that, at least for suckers, movement patterns are variable among individuals in the population, individual behavior is not fixed over the lifetime of the fish, and individuals respond differently to environmental conditions. PIT tags have a theoretically infinite

life span, and provide the opportunity for long term study of individuals and populations (Zydlewski et al. 2006). Remote detection of PIT tags can markedly increase encounter probabilities (Hewitt et al. 2010), a key limitation of many movement studies (Gowan et al. 1994), and ensure more robust inferences of key parameters. Indeed, we observed that use of traditional electrofishing techniques in the Gila River greatly underestimated population size within habitats under any but the lowest flow conditions (Booth, unpublished data). Creative study designs, involving a combination of stationary and portable PIT antennas, will provide the opportunity to investigate a variety of ecological questions at the population and individual level (e.g., diel behavior, site visitation, barrier passage, microhabitat use) on time scales ranging from minutes to decades.

In summary, with the large sample size afforded by our use of PIT telemetry, we were able to observe that the populations of suckers living in the Gila River contain a mixture of mobile and stationary individuals, with some fish exhibiting large movements while others were not detected outside of a single habitat. Furthermore, mobile or stationary behavior did not appear to be a strictly fixed trait, because individuals changed behavior from one year to the next. Movement, at least for suckers, appears to be a plastic behavior, likely due to spatial and temporal heterogeneity in resources and habitats. This result raises the possibility that mixed behaviors within a single population may exist for other taxa and in other places. Capturing this variation will be critical for designing management strategies and developing more advanced conceptual models of fish movement.

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APPENDIX: TELEMETRY REFERENCES

Number of individuals	Tag type	Reference
32	radio	Enders, E. C., K. D. Clarke, C. J. Pennell, L. M. N. Ollerhead, and D. A. Scruton. 2007. Comparison between PIT and radio telemetry to evaluate winter habitat use and activity patterns of juvenile Atlantic salmon and brown trout. Hydrobiologia 582:231-242.
5	acoustic	Carol, J., L. Zamora, and E. García-Berthou. 2007. Preliminary telemetry data on the movement patterns and habitat use of European catfish (*Silurus glanis*) in a reservoir of the River Ebro, Spain. Ecology of Freshwater Fish **16**:450-456.
9	radio	Ovidio, M., J.-claude Philippart, and É. Baras. 2000. Methodological bias in home range and mobility estimates when locating radio-tagged trout, *Salmo trutta*, at different time intervals. Aquatic Living Resources **13**:449-454.
20	radio	Popoff, N., and R. Neumann. 2005. Range and Movement of Resident Holdover and Hatchery Brown Trout Tagged with Radio Transmitters in the Farmington River, Connecticut. North American Journal of Fisheries Management **25**:413-422.
3	radio	Clough, S., and M. Ladle. 1997. Diel migration and site fidelity in a stream-dwelling cyprinid, *Leuciscus leuciscus*. Journal of Fish Biology **50**:1117-1119.
14	radio	David, B. O., and G. P. Closs. 2003. Seasonal variation in diel activity and microhabitat use of an endemic New Zealand stream-dwelling galaxiid fish. Freshwater Biology **48**:1765-1781.
29	radio	Young, M. 1999. Summer diel activity and movement of adult brown trout in high-elevation streams in Wyoming, U.S.A. Journal of Fish Biology **54**:181-189.
40	radio	Crook, D. A. 2004. Is the home range concept compatible with the movements of two species of lowland river fish? Journal of Animal Ecology **73**:353-366.
19	radio	Grabowski, T. B., and J. J. Isely. 2006. Seasonal and diel movements and habitat use of robust redhorses in the Lower Savannah River, Georgia and South Carolina. Transactions of the American Fisheries Society **135**:1145-1155.
22	radio	Taylor, P., D. B. Bunnell, J. J. Isely, K. H. Burrell, and D. H. Van Lear. 2011. Diel Movement of Brown Trout in a Southern Appalachian River. Transactions of the American Fisheries Society **127**:630-636.
19	radio	Paragamian, VL, Walters JP. 2011. Bull trout (*Salvelinus confluentus*) movement in a transboundary river. Journal of Freshwater Biology 26:65-76

6	radio	Thompson, Lisa C.; Cocherell, Sarah A.; Chun, Stephanie N.; Cech, Joseph J., Jr.; Klimley, A. Peter. 2011. Longitudinal movement of fish in response to a single-day flow pulse. Environmental Biology of Fishes 90:253-261.
49	radio	Lapointe NWR, Thorson JT, Angermeier PL. Seasonal meso- and microhabitat selection by the northern snakehead (*Channa argus*) in the Potomac river system. Ecology of Freshwater Fish 2010: 19: 566–577.
20	radio	Sarah A. Cocherell, Gardner J. Jones, Javier B. Miranda, Dennis E. Cocherell, Joseph J. Cech, Lisa C. Thompson and A. Peter Klimley. 2010. Distribution and movement of domestic rainbow trout, *Oncorhynchus mykiss*, during pulsed flows in the South Fork American River, California . Environmental Biology of Fishes 89:105-116
43	radio	Zimmer M , Schreer JF , Power M. 2010. Seasonal movement patterns of Credit River brown trout (*Salmo trutta*). Ecology of Freshwater Fish. 19:290-299

CHAPTER 4

Benthic fish as surface engineers: modification of turbulent flow, particle retention and invertebrate community dynamics

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Abstract

Benthic flow environments influence channel shape and substrate composition, retention of particles on the streambed, and hydraulic forces, all of which affect the habitat and colonization of the biota experienced by the biota. Organisms that are ecosystem engineers often create structures that can directly modify the small-scale flow environment on the stream bed. In streams of the southwestern US, catostomid fishes (suckers) create a heterogeneous and relatively long-lived honeycomb of depressions (divots) and plateaus as they forage for invertebrates in soft substrates, physically roughening the sediment-water interface. Although active digging by fish increases sediment transport and disturbs the streambed, the structures created by feeding activity increase retention of organic matter and create favorable microenvironments in the stream bed for invertebrates. We used field experiments to estimate the community consequences of divots and a combination of field and laboratory measurements over smooth and rough sediment surfaces to identify a mechanism by which particulates concentrate in divots. Field sampling showed increased accumulation of organic matter over time and high concentrations of coarse particulate organic matter in divots relative to adjacent sediment. Divots were rapidly colonized by invertebrates, with increased biomass and different taxa from the surrounding sediment. Field velocity measurements show divot fields increased bed roughness, leading to higher turbulence levels in the near-bed region, thereby increasing the potential for enhanced bedload transport. Laboratory measurements above and within a single divot showed increases in turbulent stress associated with a shear layer forming between the outer channel flow and the cavity flow within the divot. Stokes number scalings of typical particulates suggest retention in the divot is due to inertial effects caused by streamline curvature, despite increased turbulence in the near bed region. The cavity flow within a divot further concentrates particulates

in an upstream corner eddy. Local flow modifications strongly enhance the retention of particles in typically non-retentive habitats, with important consequences for the invertebrate community.

Introduction

In aquatic systems, the flow environment fundamentally structures ecological dynamics and the interaction of organisms with their surroundings (Vogel 1994, Hart et al. 1996, Hart and Finelli 1999). Flow can determine organism habitat use, colonization of microbes and invertebrates, fluxes of dissolved nutrients, and the flux and retention of particles (Nowell and Jumars 1984, Statzner et al. 1988). Flow is a dominant forcing function of aquatic ecosystems and understanding the physical—biological coupling of organisms with the flow environment can provide a richer conceptual framework for aquatic studies (Hart and Finelli 1999). Flow patterns of importance to organisms occur on a variety of scales, ranging from large-scale cyclical motions driven by tides to small-scale turbulence caused by roughness elements near the boundary layer (Vogel 1994).

Flow patterns also dictate the movement of particles through the aquatic environment (Nowell and Jumars 1984, Allan and Castillo 2007). Structures that cause large-scale modification of flow (e.g., aquatic vegetation, natural or artificial dams) make obvious changes to sediment dynamics in the ecosystem as a whole. For example, seagrass beds can redirect and reduce flow, influencing both stability of the habitat as well as photosynthetic output of the grasses themselves (Fonseca et al. 1982), while large dam structures can modify the location, storage, and transport of sediment within a river (Hazel et al. 2006). Clearly, large structures can greatly modify sediment dynamics, but the modification of the near-bed flow environment at

small scales (Nikora et al. 1998) may have less obvious yet important effects, particularly on the transport and retention of particles within habitats.

Animals can modify particle transport through flowing water environments directly via bioturbation (Statzner et al. 2003a, 2003b, Moore 2006), but physical changes to the stream bed may also have important implications for the retention and dynamics of suspended particles. In flowing waters, some ecosystem engineers like nest-building salmonids (Hassan et al. 2008) and lamprey (White 1990) or dam-building beavers (Johnston and Naiman 1987) alter both the flow environment and sediment transport in streams (Moore 2006). However, other organisms (e.g., invertebrates; Pringle et al. 1993, Zanetell and Peckarsky 1996) may cause more subtle changes to the stream bottom compared with beavers or salmon, yet still modify sediment transport and flow dynamics near the stream bed (Statzner et al. 2000).

Previous studies have improved our understanding of the effects of flow on ecological characteristics (Statzner et al. 1988, Carling 1992), but have pointed out that integration of flow and ecology is still in its infancy. In that context, the creation of physical structures, like feeding scars or spawning depressions, most certainly modifies flow patterns near the stream bed and could thereby have important consequences to ecosystems. Feeding divots (or similar structures like nests and burrows) are regularly found in marine and estuarine environments (e.g., feeding depressions by rays; VanBlaricom 1982, Yager et al. 1993), and likely are also common in streams with fine sediments and benthic feeding organisms. In marine environments, feeding depressions have been shown to alter boundary layer dynamics compared to a smooth bed, creating potential retention structures for coarse particulate organic matter and novel habitat structures for invertebrates (Yager et al. 1993).

While there is some evidence that depressions can serve to concentrate coarse particulate organic matter (CPOM) (Yager et al. 1993), the flow characteristics and mechanisms by which depressions retain particulates deserve more investigation. In streams, the transport and retention of CPOM at small spatial scales is influenced by the presence of in-stream structures (Webster et al. 1994, Small et al. 2008); in cobble habitat, the substrate itself acts as widespread retentive structure, while in soft sediment habitats, retention structures such as woody debris typically provide relatively little habitat surface compared to the stream bottom, but are an important source of animal production (Benke et al. 1985). Biogenic depressions or divots represent a potentially abundant structure that may promote particulate retention in the streambed and provide habitat for other organisms.

We observed that the Sonora sucker, *Catostomus insignis*, a benthic feeding catostomid fish common in streams of the southwestern United States, creates divots in soft bottom sediments as it feeds on invertebrates and detritus. These depressions can be extremely abundant in depositional habitats, as well as sandy runs (as many as 220 divots per m^2), and can cause measureable sediment displacement (up to 2.38×10^4 cm^3/m^2; Chapter 1). However, feeding disturbance by these fish is patchy in space and time, and during low flow periods, divots can be long-lived (weeks) unless a fish subsequently feeds in that area and displaces adjacent sediments, filling in the depression. Although the fish directly affect invertebrates via consumption, their feeding behavior may also create microhabitats more favorable for benthic prey taxa, thereby indirectly affecting benthic community dynamics. In this context, fish feeding could have two distinct effects: direct consumption of invertebrates and ecosystem engineering at the microscale, which could result in a positive feedback to the predators. The general goal of this study was to understand the mechanisms and consequences of sucker engineering of the stream bed, and

answer the following specific questions: 1) what mechanisms cause divots to capture and retain particulate matter, and 2) what are the consequences of divots for the retention of organic matter, creation of benthic invertebrate habitat, and the composition of the benthic community? We hypothesized that modifications to the near bed flow are responsible for the enhanced retention of organic matter and that divots represent a favorable habitat for invertebrates compared with the adjacent homogeneous smooth sandy bottom.

Methods

Our field site was on the West Fork of the Gila River in southwestern New Mexico at the Heartbar Wildlife area, near the confluence of the West and Middle Forks of the Gila River. The upper Gila River is a tributary to the Colorado River that originates in the Mogollon Mountains of western New Mexico and is one of the few remaining unregulated rivers in the western US. The Sonora sucker is abundant in the West Fork of the Gila and typically represents the majority of fish biomass in this section of the river (90% of the fish biomass in 2008; Chapter 2). The study reach is predominantly riffle-pool with wide shallow runs and occasional beaver dams. Estimated median discharge in June 2010 was 0.62 m^3/s (range 0.20-3.05 m^3/s). Fish-created divots are a common feature in soft sediments (i.e., sand, silt, gravel) of the Gila River, and are roughly cylindrical depressions in the streambed, which range in size from 1 cm wide and 0.4 cm deep to 40 cm wide and 6.8 cm deep (Chapter 1). The inter-divot distance in the field is highly variable, ranging from centimeters to meters. All field sampling and flow measurements occurred during June 2010. Laboratory experiments occurred during June 2011.

Consequences of divot creation

Due to the high prevalence of divots and the high frequency of their creation (i.e., new divots on top of old divots, so that it was unclear when a patch of habitat had last been disturbed), it was not possible to estimate directly how divoted sediments differed from those that were undisturbed. Instead, we estimated how divots change organic matter retention and invertebrate abundance in the streambed using artificially created divots made from 120 mL specimen cups (0.02 m^2 opening, similar to natural divots) at three sites in the river. Locations for sampling sites were distributed throughout our 2 km study reach (200-1400 m apart; see Chapter 1 for further description), based on similar sediment characteristics (primarily sand mixed with silt) and adequate room on the streambed with similar flow characteristics for installing sampling devices. At each of three sites, 20 cups were placed so the opening was flush with the surface of the sediment in a four by five array. Five cups were randomly collected without replacement at each sampling interval of 1, 3, 5, and 10 days. In addition, on day 5 at each of the three sites, five replicate sediment samples were collected from the streambed adjacent to the specimen cups. To compare ambient organic and invertebrate content with artificial divot samples, we scooped sediment into a specimen cup while a fine mesh net (0.3 mm) was held directly downstream to capture escaping invertebrates and its contents recombined with the sediment sample. Samples were immediately frozen for processing in the laboratory. Each sample was slowly thawed and then filtered through 1 mm, 250 µm, and 45 µm mesh filters. The 1 mm and 250 µm fractions were sorted under a dissecting microscope removing all invertebrates, then all fractions were dried at 70 °C, weighed and combusted at 450 °C for 4 h, rewetted to restore water of hydration (Wallace et al. 2006), dried overnight at 70 °C, and reweighed to measure organic matter content. Invertebrate taxa were identified to the lowest

practical taxonomic level (typically family), and then dried on preweighed filters at 60 °C and weighed to determine dry biomass. Due to the low frequency of occurrence, large invertebrates (> 7 mm, primarily Odonata and Tricoptera) were not included analyses of biomass. We tested for differences between artificial divots and adjacent substrates on log-transformed organic matter: dry mass ratios using a one-way ANOVA and used AFDM as a covariate in an ANCOVA to investigate the relationship of invertebrate abundance to AFDM at different sampling sites. All statistics were computed using JMP 8.0 (SAS).

Flow measurements

We employed acoustic Doppler velocimeters (ADV) to measure flow and turbulence near the stream bed (Voulgaris and Trowbridge 1998). In the field, a Vector ADV (NortekUSA, Boston, MA) was used to measure flow near natural divots, artificially created divots, and above non-divoted stream bed. For laboratory experiments, a Vectrino ADV (NortekUSA, Boston, MA) was used. Both instruments measure the velocity of particles in a remote sampling volume based upon the Doppler shift effect, with the primary differences being a much larger and more remote sample volume for the Vector, and a higher sample rate (up to 200 Hz compared to 64 Hz) and addition of a fourth receiver on the Vectrino.

The ADV head was mounted to an adjustable stage for vertical positioning and attached to either a PVC frame (field) or moveable carriage on the flume (laboratory; Appendix Figure1). In the field, the frame was positioned above a section of the river bed and two or three measurements were taken at elevations 0.05, 0.10 and 0.15 m (± 0.01 m) from the bed (water depth permitting). Measurements were made at several locations where divots were abundant within a 3 km section of the West Fork Gila River. At each site, measurements were first made directly above a divot and then for comparison with non-divoted areas we either experimentally

filled and smoothed the divot or repositioned the ADV over a nearby non-divoted region. Data were recorded for approximately 15 minutes at 16 Hz, resulting in 14,000 data points for analysis at each height above the bed. In the laboratory, we collected 14 evenly spaced data points from within the divot to 0.10 m above the stream bed. Velocities were sampled at 200 Hz for 10 minutes, resulting in approximately 120,000 data points for analysis at each height.

Laboratory experiments were conducted in an 8 m long recirculating flume in the DeFrees Hydraulics Laboratory at Cornell University. The flume was fitted with a recessed chamber (described fully in Rusello, unpublished dissertation, Appendix Figure 1) for holding sediment cores. Flow was powered by two variable-speed centrifugal pumps. Flow depth was established under still water conditions at 30 cm, approximating depths encountered in the Gila River. The laboratory target flow speed was 0.08 m/s, a value within the range of flows typically encountered in divoted areas of the Gila River.

An artificial sediment core was constructed by mixing fine playground sand (approximately 70% of final volume) with a fine mud (predominantly clay with some silt and fine sand) excavated from a lake bottom. The sediment mixture was similar to that observed in frequently divoted areas of the Gila River. The sediment core was allowed to settle for three days before experiments were performed. A divot was formed by scooping out a section of the core in a manner that resulted in a depression similar to the feeding scars of Sonora suckers in the Gila River. A second experiment using an artificial divot (120 mL plastic sample cup, 0.02 m^2 opening) was conducted by burying the cup in the sediment core so its lip was flush with the sediment surface. Prior to velocity measurements, flow visualizations were performed using water soluble red dye #40 and organic debris. A mass of dye was injected into the divot prior to starting flow in the flume and photographed at 1-2 second intervals for one minute after flow

began. Organic debris was introduced into the flume including > 5 mm pieces of aquatic plant material obtained from a local water body; we released particles into the flume 2 m upstream directly upstream of the divot.

Flow data analysis

Analysis was carried out using numerical packages Matlab (Mathworks, Natick, MA) and Numpy/Scipy (Enthought Python Distribution, Austin, TX). Routine data quality checks were performed, including discarding very low correlation (less than 40%) and signal-to-noise ratio (less than 5 db) data points (Rusello et al. 2006). An iterative, adaptive Gaussian filter was used to remove outliers (Cowen and Monismith 1997). All statistics (mean, root mean squared velocity, etc.) were calculated on the screened velocity time series. Measured velocities were decomposed into a mean and temporally fluctuating component following the Reynolds decomposition:

$$u(t) = \bar{u} + u'(t) \qquad \text{Equation 1}$$

Mean velocities $\bar{u}$ were calculated at each elevation by averaging in time. Parameters are defined in Table 4.1. The fluctuating component $u'(t)$ was characterized by the root-mean-square (RMS) value, referred to here as the turbulence intensity (essentially the standard deviation of the signal). Reynolds stresses (a measure of stress due to the random turbulent fluctuations; i.e., a co-variance term such as $\overline{u'w'}$) were calculated for each valid velocity measurement and then averaged.

The mean velocity profile is expected to follow the Law of the Wall:

$$u^+ = \frac{1}{\kappa}\ln z^+ + \beta \qquad \text{Equation 2}$$

Table 4.1. Definition of symbols used in equations.

Symbol	Definition
u	Streamwise velocity
v	Cross-stream velocity
w	Vertical velocity
$\overline{u'v'}$, $\overline{v'w'}$, $\overline{u'w'}$	Reynolds shear stress components
$u'(t)$	Fluctuating component of velocity
u^+	Dimensionless velocity
u^*	Shear velocity
z^+	Elevation above the bed
Z^+	Adjusted elevation above the bed
z_0	Zero plane offset
ν	Kinematic viscosity
κ	Von Kármán constant
β	Roughness constant, assigned value of 5.0
$\frac{\Delta U}{u_{*+}}$	Roughness function
h	Roughness element height
h^+	Roughness Reynolds number
ρ	Fluid density
D_{50}	Median diameter of particles
τ	Relaxation time of a particle
U_0	Fluid velocity of the flow well away from an obstacle
$\frac{w_s}{\kappa u_*}$	Particle Rouse number
L	Roughness element spacing
d	Roughness element diameter

The dimensionless velocity $u^+ = \frac{\bar{u}}{u_*}$, where u is the velocity parallel to the wall (i.e., the boundary of the fluid region) and u_* is the shear velocity, and dimensionless elevation above the bed $z^+ = \frac{zu_*}{\nu}$, where z is the elevation above the bed and ν is the kinematic viscosity. κ is the Von Kármán constant and the constant β was assigned a value of 5.0 for a smooth wall. Elevation (height above the stream bed) required adjustment because the flow separates from the boundary at the divot lip, forming a shear layer with the divot cavity flow. In the above equation, this elevation offset was accounted for by replacing z^+ with $Z^+ = \frac{(z-z_0)u_*}{\nu}$, where z_0 is the zero plane offset. Mean velocity profiles were fit to Equation 2 using an iterative least squares approach. The initial estimate of the elevation adjustment z_0 was half of the divot depth, while u_* was estimated as 5% of the free stream velocity.

To allow for roughness effects, Equation 2 was modified with an additional term known as the roughness function (Raupach et al. 1991), $\frac{\Delta U}{u_{*+}}$, subtracted from the right hand side of Equation 2. A larger value of the roughness function indicates a rougher sediment surface and greater flow modifications. The relationship between $\frac{\Delta U}{u_{*+}}$ and physical roughness height h, is expected to be log-linear (Raupach et al. 1991). In terms of flow variables, a rougher surface will generate higher turbulence levels in addition to the mean flow modification inherent in a non-zero value of $\frac{\Delta U}{u_{*+}}$. Confidence intervals were estimated on flow statistics using the bootstrap method (Efron and Tibshirani 1993) with 1000 replicate statistics.

Results

Consequences of divot creation

Artificial divots rapidly collected particulate matter (Figure 4.1). Within a day, artificial divots contained 239 to 490 g/m^2 dry mass and by day 10 divots contained 700 to 1250 g/m^2. Dry mass and ash free dry mass (AFDM) were predominantly composed of large particles (> 250 µm). Large organic particles were primarily of terrestrial origin and consisted of leaves, pine needles, and twigs, although some filamentous algae were also collected in the divots. Organic matter (AFDM) made up about 5-10% of the total mass in artificial divots, but typically composed the majority of the volume in the divot. Although divots contained similar amounts of organic matter to the ambient sediment (30-215 g/m^2), artificial divots contained proportionally more organic matter per unit dry mass than adjacent sediments (Figure 4.2A, $F_{3,19}$=42.4, $p<0.0001$). Particulate organic matter was typically not found on non-divoted surfaces, but was buried underneath the surface layer of the sediment.

The three sites differed in invertebrate biomass (Figure 4.1C), but we observed consistently higher invertebrate biomass in artificial divots than in ambient sediment (Figure 4.2B, $F_{3,19}$=6.18, p=0.0041). Invertebrates rapidly colonized divots, but individual taxa showed distinct trajectories (Figure 4.1D). Hydracarina (water mites) were abundant on day 1, but declined steeply over time. Other taxa, primarily Ephemeroptera nymphs (R^2=0.66, $F_{4,51}$=25.0, $p<0.001$), Diptera (primarily chironomid) larvae (R^2=0.59, $F_{4,51}$=18.4, $p<0.001$), and Coleoptera (elmid) larvae (R^2=0.65, $F_{4,51}$=23.9, $p<0.001$), were significantly correlated with increased organic matter trapped in the divots and abundance increased over time ($p \leq 0.05$). Artificial divots also contained different invertebrate taxa than ambient sediment (Figure 4.2C).

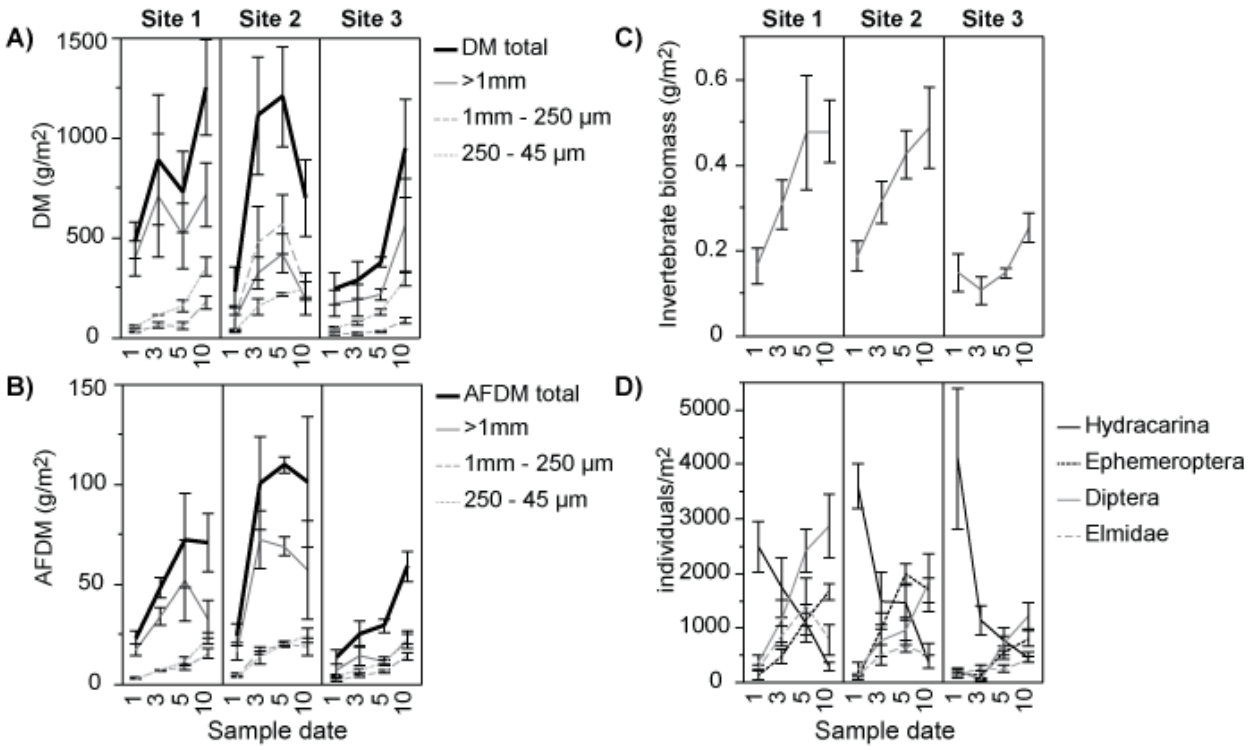

Figure 4.1. Capture of organic matter and colonization of invertebrates trajectories for artificial divots at three sites within the West Fork Gila River over a ten day period. A) Total mass, B) ash-free dry mass, C) invertebrate biomass, and D) abundance of dominant invertebrate taxa. Data shown are means of five artificial divots on each date ± 1 s.e.

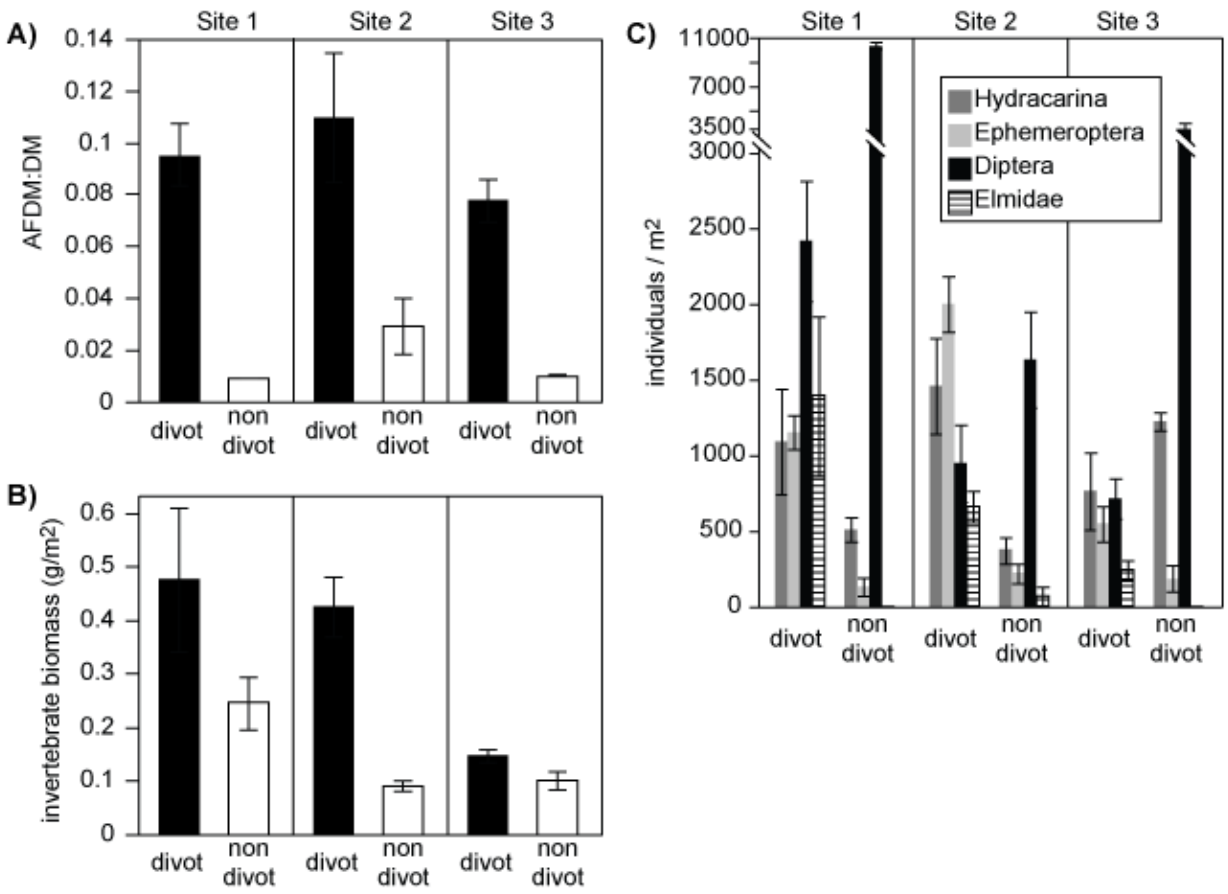

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Figure 4.2. Comparison of A) the proportion of ash free dry mass to total mass, B) invertebrate biomass, and C) abundance of dominant invertebrate taxa in non-divoted sediment cores and artificial divots after 5 days of incubation at each of three sites in the Gila River. Data are means ± 1 s.e., statistical tests are provided in the results section. Note the change in scale at the break on the y-axis.

Chironomids were more abundant in ambient sediment ($F_{3,19}$=17.2, p<0.0001) but mayflies $F_{3,19}$=20.5, p<0.0001) and elmid beetle larvae ($F_{3,19}$=4.6463, p=0.0134) were significantly more abundant in divots than ambient sediment.

Field flow measurements

Comparing flow measurements above a divot to the filled and smoothed divot at the same site showed no significant difference in any flow statistic at the lowest measurement elevation of 0.05 m above the stream bed. Mean stream-wise velocities differed by only a few mm/s with narrow confidence intervals of 0.005 m/s. Turbulence intensities and Reynolds stresses showed similar trends in root-mean-squared values and confidence interval widths, indicating similar flow patterns between divots and smoothed stream bottom. However, we observed statistically significant differences when comparing two physically separated measurement locations at a site (i.e., when the instrument frame was moved from directly above a divot to a smooth sediment surface nearby). Those differences could be attributed to a variety of sources, but seem likely to be a result of measurement location rather than the presence or absence of a divot, given the minimal difference observed when filling and smoothing a divot. Where it was possible to fit velocity profiles (i.e., when water depth permitted velocity measurements at three elevations above the sediment), $\frac{\Delta U}{u_{*+}}$ took on a non-zero value on the order of 10, indicating the overall divot field substantially roughened the sediment surface and modified the flow.

Turbulence and Reynolds stress levels, when scaled with u_* estimates (5% of free stream velocity) to allow comparison to canonical expectations, were high relative to smooth wall values, also indicating roughness effects from the divot field. Our analytical techniques cannot separate sources of turbulence, but we expect that divots are probably not the sole source, with

additional sources of upstream turbulence such as turbulent wakes generated by physical structures in the stream. Among all locations in the stream where we measured flow, stress at the stream bed was 0.02-0.10 Pa, with the turbulent stress estimate of - ρ $u'w'$, where ρ is the fluid density, often at the higher end of this range owing to the rougher sediment surface.

Laboratory flow measurements

Flow visualization revealed that most of the injected dye was quickly removed from a divot, but a parcel remained at the upstream divot wall for several minutes, slowly diffusing out into the main flow (Figure 4.3). We observed a well-defined eddy within an artificial divot cup and less defined, but still present, circulation in natural divots.

Streamlines of water flow, visualized by the dye, depressed slightly when above a divot (cf. Figure 2a of Shankar and Deshpande 2000) but resulted in minimal accumulation of dye within the cavity. Debris consisting of dried plant material released upstream of a divot was transported primarily as bed load and quickly settled into the divot, occupying a space near the upstream wall similar to the initial mass of dye injected into the divot. This corner eddy concentration was consistent with expectations given the fairly quiescent conditions expected within the divot (Nowell and Jumars 1984, Abelson and Denny 1997, Shankar and Deshpande 2000) and typical cavity flow behavior.

The divot shape and depth were stable and there was little observable change over six hours of data collection. Using the acoustic distance measurement of the Vectrino ADV, the divot depth was measured multiple times relative to the smooth sediment surface 0.16 m upstream. Divot depth (N=4, accurate to within 5.0×10^{-4} m; Rusello, unpublished dissertation) was 0.023 m (mean) and 0.024 m (median).

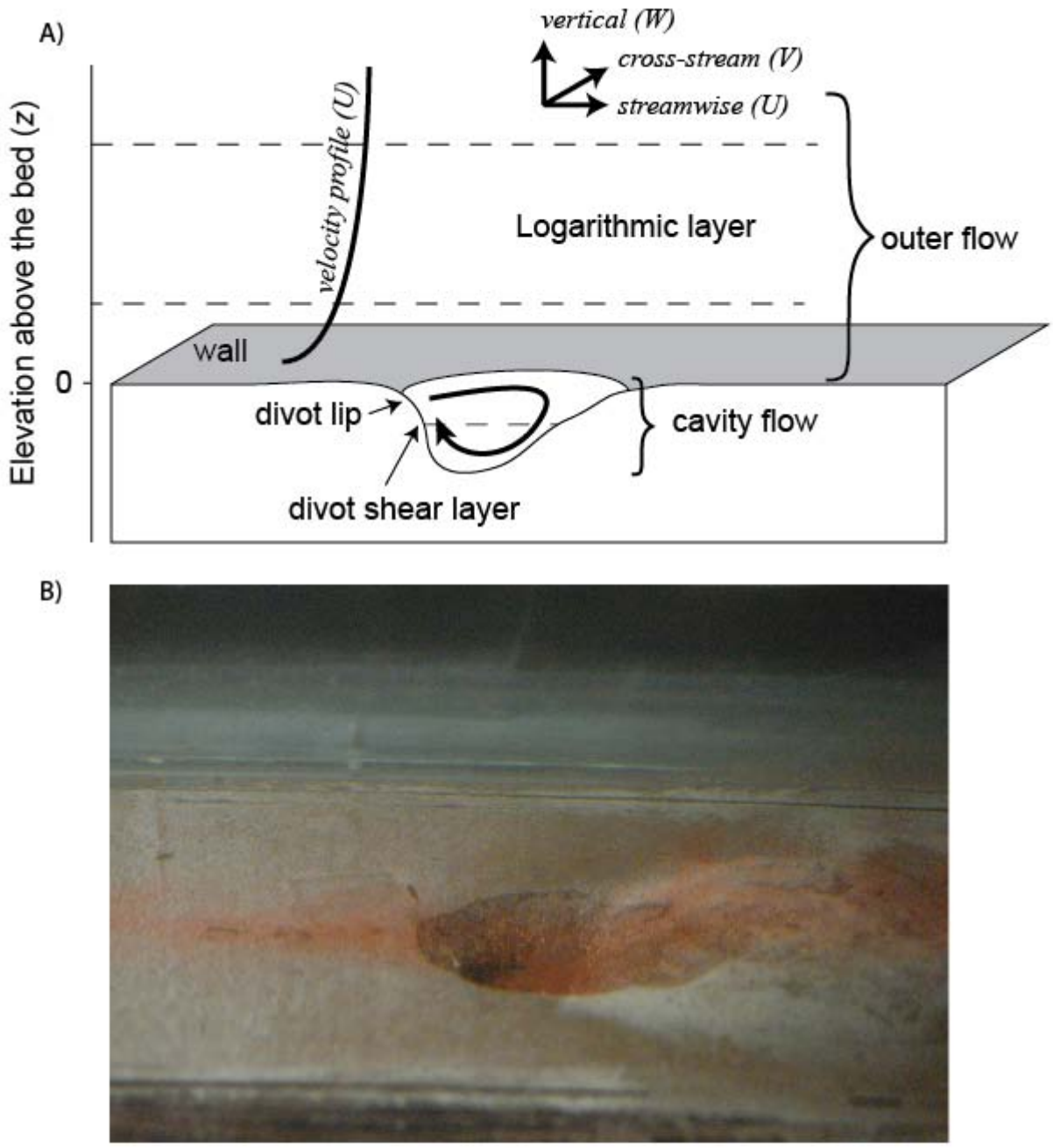

Figure 4.3. A) Schematic of key flows and structures for flow measurements and visualization. B) Flow visualization over divot in the laboratory. Photo shows a dye streak curving into the divot. Some captured debris is visible near the front wall of the divot. Flow is from left to right.

The flow upstream of the divot was expected to be a hydraulically smooth turbulent boundary layer (in contrast to the rough wall flow expected and observed in the river itself). The sand used in constructing the artificial core has a D_{50} (median diameter) = 0.30 mm. We estimated u_* at 5% of the free stream velocity of 0.08 m/s (approximately 0.004 m/s), yielding a roughness Reynolds number, $h^+ = \frac{D_{50}\, u_*}{\nu} \approx 1$, well below the threshold for transitional or fully rough boundary layer flow (≈ 5).

The Law of the Wall optimal parameters were $u_* = 4.2 * 10^{-3}$m/s and $z_0 = 0.016$ m, approximately 2/3 of the mean divot depth. Visual observations during the experiments and prior work on lid driven cavity flows (i.e., flow within the cavity is driven by flow at the "lid" of the depression; Shankar and Deshpande 2000) suggest the outer flow remains coherent to approximately 50% of the cavity depth for broad, shallow depressions. u_* was largely insensitive to the value of z_0 as long as an appropriate range of data was used for the fit.

Normalized mean velocity profiles for streamwise (u), cross-stream (v), and vertical (w) velocity show the influence of the depression and its flow on the mean profile (Figure 4.4). There was a gradual transition to a zero velocity within the divot rather than the higher shear expected from hydrodynamic theory below the logarithmic region of the velocity profile caused by the presence of a solid boundary. The flow outside of the divot (the outer flow) drove the formation of an eddy within the divot (called lid driven cavity flow). The divot eddy was expected to rotate clockwise in the streamwise (i.e., downstream) direction. Because the outer flow is faster than the divot eddy rotation, a shear layer develops between the two. The mean streamwise velocity profile suggested that the middle of the shear layer was near z = -0.01 m with a thickness of approximately 0.01-0.02 m. The size of the Vectrino ADV sample volume (0.007 m) is similar to the approximate shear layer thickness, resulting in spatial averaging across most of the shear

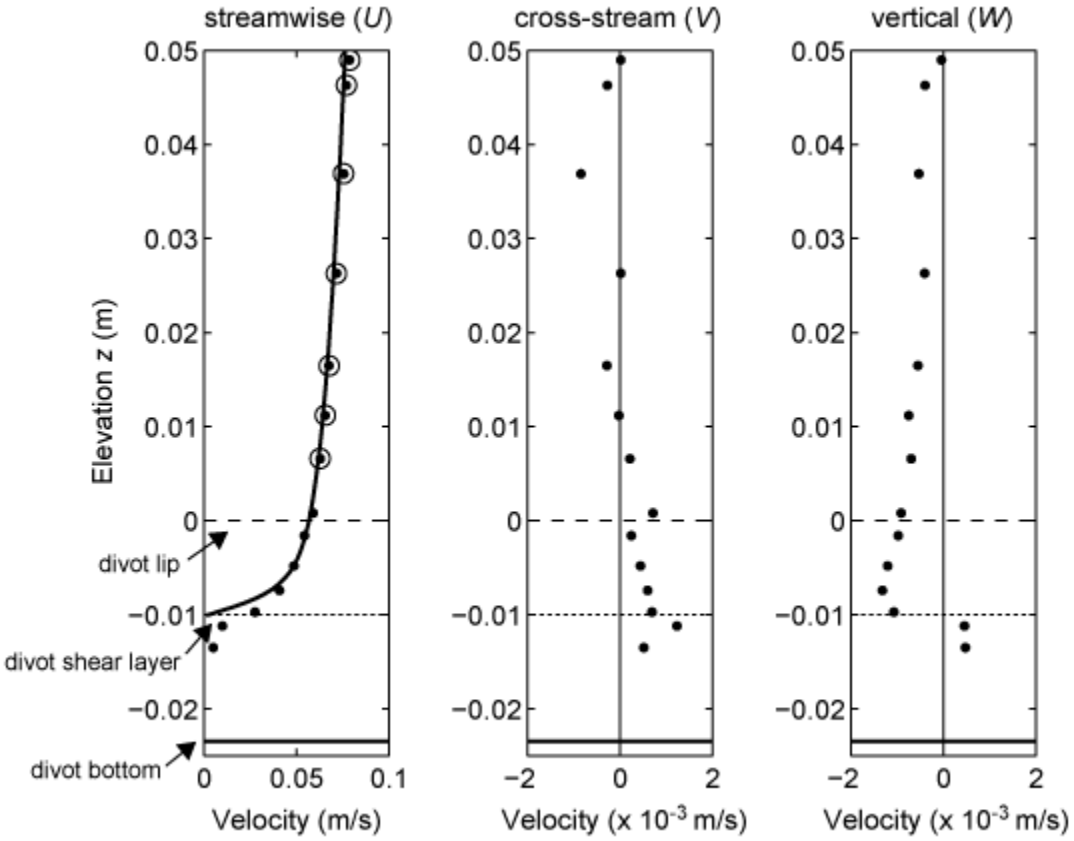

Figure 4.4. Plots of mean velocity profiles for streamwise (*U*), cross-stream (*V*), and vertical flow (*W*). Circled points in the streamwise velocity profile indicate the log-law portion of the flow. Elevations (z^+) are relative to the flume bottom, with negative elevations representing data points taken below the lip of the divot. Solid line in streamwise (*U*) is the direct numerical simulation results of Spalart (1988), vertical lines in cross-stream (*V*) and vertical (*W*) profiles are zero reference.

layer. The rotational center of the eddy is approximately 0.015 m from the divot bottom from the location based on the measured zero velocity point in the streamwise profile. The eddy was expected to conform to the boundaries of the divot, so the core region is likely oval in shape.

The expected peak in streamwise turbulence intensity and the overall mean velocity profile was shifted downward vertically below the logarithmic layer and occurred below the lip of the divot. The observed peak was much broader with a larger magnitude than expected (Figure 4.5), and is likely a superposition (or interaction) of the expected smooth wall peak and the divot shear layer. The divot's effect on the other turbulence intensity components was to eliminate any decrease in turbulent intensity levels below the logarithmic layer as would be expected.

Reynolds shear stress levels (force vector perpendicular to surface normal vector) showed effects from the presence of the divot and shear layer as well (Figure 4.6). The $\overline{u'v'}$ shear stress component (Figure 4.6) changed sign within the divot several times, indicating potential three dimensional effects (e.g., a horizontal rotation caused by an asymmetrical divot), with a peak in magnitude coinciding with the middle of the shear layer. The $\overline{v'w'}$ stress component decayed almost to zero at the middle of the shear layer before increasing below it. The $\overline{u'w'}$ component increased significantly from the outer flow value, starting at the divot lip and reaching a maximum value two times higher than the outer flow value at the middle of the shear layer. It decayed quickly below this value in the core of the divot eddy.

Compared with measurements made 0.16 m upstream of the divot (not shown), turbulence intensities and stresses remained at or above outer flow values in the upper portion of the divot, only decaying in the eddy core. Measurements in the bottom half of the divot were not made due to limitations of the ADV in measuring close to solid boundaries. While not directly measured, the presence of an upstream wall eddy in the divot was confirmed during flow

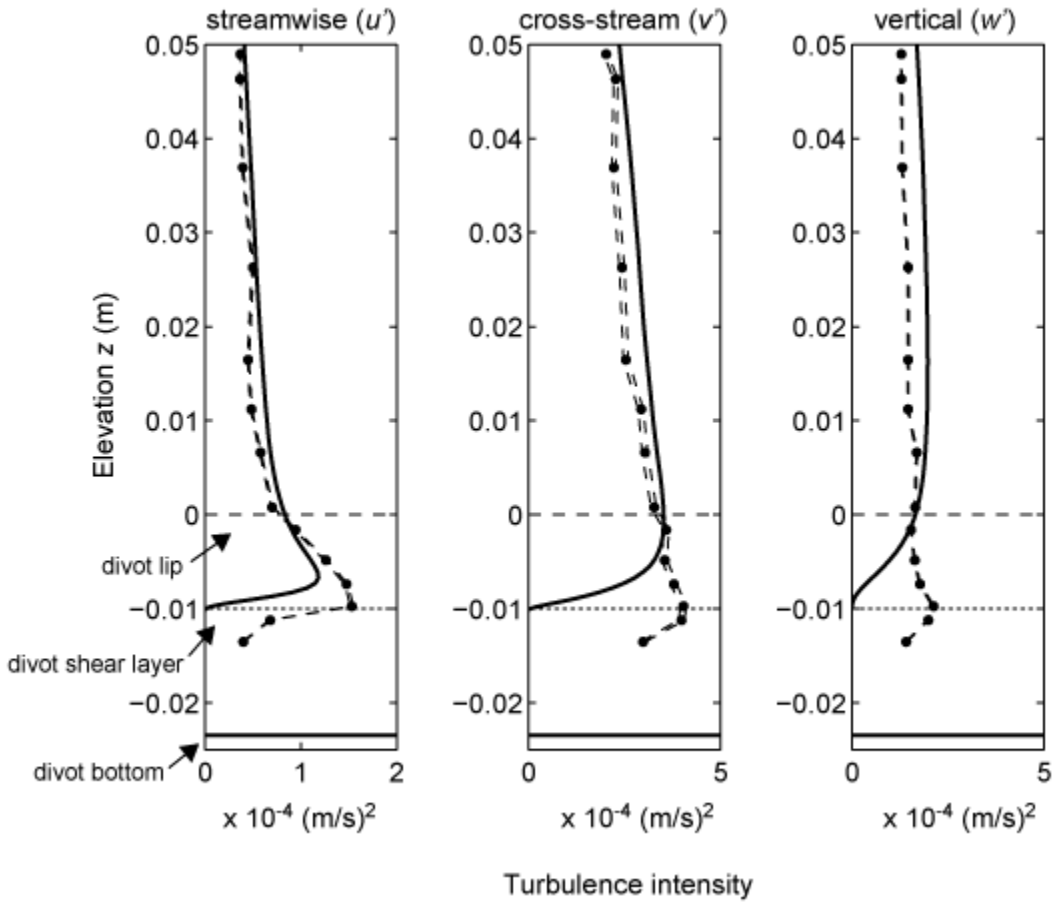

Figure 4.5. Turbulence intensity profiles for streamwise (*u'*), cross-stream (*v'*), and vertical (*w'*) velocities, where *z+* is the elevation relative to the flume bottom, negative *z+* values indicate measurements within the divot. The direct numerical simulation results of Spalart (1988) indicated with a solid line and the dashed lines indicate 95% confidence intervals.

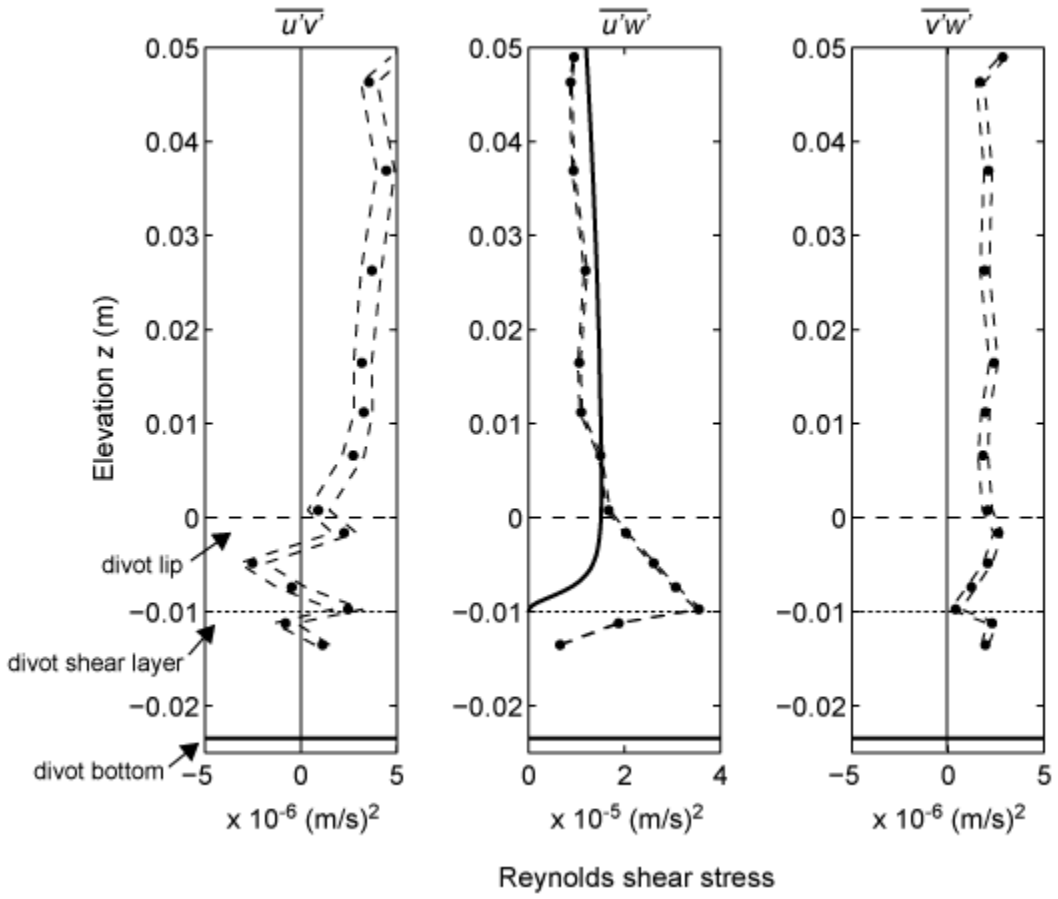

Figure 4.6. Reynolds stress profiles for $\overline{u'v'}$, $\overline{u'w'}$, and $\overline{v'w'}$. The direct numerical simulation results of Spalart (1988) for $\overline{u'w'}$ is shown as a solid line and dashed lines indicate 95% confidence intervals. Vertical lines in $\overline{u'v'}$ and vertical $\overline{v'w'}$ profiles are zero reference.

visualizations. Comparisons between the measurements upstream and directly above the divot show local effects of the divot were primarily confined to elevations within half of the divot depth measured relative to the upstream sediment surface location, primarily affecting vertical mean velocity, turbulence intensity and the $\overline{u'w'}$ shear stress component.

Quantitatively as well as qualitatively, the flow above and within the artificial divot was not different from that of the natural divot (data not shown). A peak in the streamwise turbulence intensity as well as increased turbulent stress occurred within the divot and with a similar magnitude to that observed in the sediment divot. Velocity decay was more gradual due to the greater depth of the artificial divot.

Discussion

We found that artificial divots caused the streambed to capture particulate organic matter. Although we did not detect differences in organic matter standing stocks between artificial divots and the ambient stream bottom, divots accumulated more organic matter per unit sediment mass than the surrounding sediments. We suspect that much of the CPOM biomass collected within the ambient stream bottom sediments had been previously captured in divots, which were subsequently covered with sediment by adjacent feeding activity thereby burying the concentrated organic matter. Indeed, we observed layering of CPOM and inorganic sediment in our artificial divots placed within the river, suggesting that this is a potential mechanism for incorporation and longer term retention of CPOM in the stream bottom.

The habitat structure of the divot, as well as the quickly accumulated organic matter, potentially provides a favorable habitat for invertebrate primary consumers in soft bottom sediments. In some stony bottom streams, invertebrate biomass can be strongly correlated with

CPOM (Flecker 1984), particularly when food is limiting (Peckarsky 1980). Fine substrates tend to contain lower biomass and different, smaller-bodied fauna than coarse substrate (burrowing fauna; Mackay 1992). Although divots do not change substrate particle size, they create roughness elements, interstitial space, and increased organic matter which can be exploited by additional invertebrate taxa, thereby increasing their abundance and biomass. We observed that divots were quickly colonized by water mites (Hydracarina) and, as organic matter increased, by mayflies and elmid beetle larvae. In ambient sediment samples, chironomids dominated the invertebrate community while elmid beetles and mayflies were rare, suggesting that the divots provided a more favorable habitat that was not available for those taxa in the non-divoted areas.

In addition to high concentrations of CPOM, near-bed hydraulic conditions can strongly influence the invertebrate assemblage (Statzner 1988, Davis and Barmuta 1989, Growns and Davis 1994, Mérigoux and Dolédec 2004). Divots may have provided regions where the energetic costs to invertebrates of staying in place was reduced because of the near zero velocity in the central eddy of the cavity flow. In addition to particulates, divots also potentially capture drifting invertebrates entrained in the flow.

Our artificial divots provided a reasonable surrogate for natural feeding depressions in terms of flow dynamics and the CPOM capture potential of the divot, but the physical structure of the artificial divots likely obstructed foraging by fish on its contents. Thus, our invertebrate abundance and biomass patterns are likely the combined result of fish exclusion, capture of particulates, and changes in flow patterns. Natural divots potentially have lower invertebrate biomass than we observed in artificial divots because Sonora suckers also feed in already formed divots (although not more frequently than non-divoted habitat:; 9 feeding instances in already formed divots out of 20 total feeding instances observed) and the invertebrates found in divots

and the undisturbed bottom are those typically found in stomachs of Sonora suckers (Clarkson and Minckley 1988, Pilger et al. 2010). However, we do not expect that increased invertebrate abundance in artificial divots is primarily due to fish exclusion, given our findings that divots rapidly concentrate organic matter and are colonized by invertebrates more rapidly than the frequency at which suckers return to feed in habitat patches (> 1-3 days, Booth, Chapter 1).

Local flow effects, combined with particle transport dynamics, provide a plausible explanation for the CPOM capture we observed in divots. The transport of organic debris in a stream is controlled by several different aspects of the flow. Suspended particles may settle out of the flow if their settling velocity is large enough to counteract any dynamic lift forces they experience (Rubey 1933). Particle behavior in a turbulent flow is further controlled by turbulent vortices, which have been shown to actively transport particles to and from the bed (Kaftori et al. 1995). Once particulates encounter the bottom, they are subject to a variety of turbulent motions, including transport as bed load, saltation (i.e., temporary transport by the flow), and resuspension. (Francis 1973)

Bed load particles may also encounter bed forms that alter the flow, creating regions where particles are concentrated relative to a smooth boundary because of a change in flow conditions. Qualitative predictions suggest flow within a depression will be a region of reduced shear stress and increased residence time for mobilized particulates (Nowell and Jumars 1984). Yager et al. (1993) identified gravitational settling as a dominant mechanism of particle deposition within experimentally created depressions in a flume, observing that deposition rates increase over a range of increasing divot aspect ratio (depth/diameter) and divot Reynolds number based on diameter.

We observed higher turbulent shear stress, specifically $\overline{u'w'}$, above both a single divot and a field of divots compared to non-divoted substrate. The elevated turbulent stress observed in the field will mobilize a broader range of particulate matter and limit the settling rate of suspended particulates. Coupled with u_* estimates, Rouse numbers indicate that CPOM will be mobile and should be primarily suspended load, although there is also likely bed load and saltation transport as well. Yager et al. (1993) suggested that gravitational settling is an important mechanism for concentration of particulates in divots. However, gravitational settling may be slow relative to transport—the highest settling velocity for organic particles based on prior studies is 5 mm/s (Hannan 1984). If a particle starts at $z = 0$ as bed load with a divot depth of 25 mm, it would need about 5 seconds to settle from the divot lip to the deepest point, and for a 1 mm/s settling velocity the time needed to settle into a divot would be 25 seconds. Given streamwise velocities of 0.08 m/s, particles would not have sufficient time to settle into the divot prior to being transported downstream by the flow. Gravitational settling could move particulates into the divot, but should not concentrate in one region instead of another. Our results suggest that for particles with low settling velocities inertial forces appear to be the primary mechanism causing settling. Therefore, our measurements of increased turbulent stress within the divot directly contradict the prediction of Nowell and Jumars (1984), which hypothesized divots are regions of reduced shear stress.

Inertial effects due to the size and density of typical particulates appear to be the principle mechanism resulting in concentration of CPOM within divots. Flow visualizations showed little accumulation of dye in a divot, suggesting the outer flow and cavity flow have minimal exchange across their shear layer. However, debris readily accumulated in the divot. Stokes numbers ($\tau\ U_0$ / particle diameter), a measure of how closely particles follow flow streamlines,

for smaller particles (mean diameter 5 x 10^{-4} m), are > 1 in the outer flow but < 1 in the cavity. These Stokes numbers indicate that in the outer flow where streamlines are parallel to the bottom and experience minimal curvature, particles will be transported predominantly with the flow. Above the divot where the streamlines curve down into the divot, these particles will have difficulty following the streamlines. They will easily fall out of the flow, and based on flow visualization, their trajectories will carry them across the shear layer where they are entrained in the cavity flow. While gravitational settling might play a role in transport across the shear layer, based on literature settling velocities (0.5-5 x 10^{-3} m/s; Hannan 1984, Marcus and Fuller 1986 for larvae and eggs; organic matter and fine sediment flocs < 1 x 10^{-3} m/s; Patten et al. 1966, Stabel 1987, Voulgaris and Meyers 2004) and the range of u_* determined for field and laboratory conditions, particle Rouse numbers (which determine how particles will be transported in a flowing fluid; $\frac{w_s}{\kappa u_*}$) are well below the threshold for inorganic sediment motion and indicate that organic particles are primarily transported as suspended load.

While we were unable to measure the local effects of a single divot under natural conditions, we observed that flow over a field of divots is rough. In laboratory experiments roughness element size, spacing, and shape modify flow patterns in fully rough, turbulent pipe flow (Scaggs et al. 1988). As the ratio L/d (where L is roughness element spacing and d is element diameter) increases (roughness elements spaced further apart), roughness effects decrease. For ratios of L/d between 2 and 4, the influence of roughness decreases from 5 times to 2.5 times greater than friction drag, approaching an asymptote of ≈ 1.5× friction drag for L/d > 10 when compared to a smooth wall. For the typical divot in the Gila River, the ratio $L/d \approx 2$, indicating a potentially large increase in drag relative to a non-divoted bed. Yager et al. (1993) showed deposition rates to conical pits was primarily dependent on the flow regime (i.e.,

hydraulically smooth, transitional, or fully rough) characterized by the roughness Reynolds number, showing increased capture rates of particulates when surface roughness upstream of a divot was increased with the addition of gravel. Thus, while one divot can successfully capture CPOM, the roughness effects of a field of divots may amplify capture rates.

While we do not have estimates of how many divots a single fish makes each day, it is likely that overall divot density is related to density of fish feeding in a habitat. We observed that initial divot size increases with fish size, because newly formed divots (i.e., formed from a single feeding action) tend to conform to the shape of the fish's head. While subsequent feeding often enlarges divots, we expect that the size distribution of divots may be explained in part by the size distribution of fish creating them. Although *C. insignis* is currently abundant in the upper Gila River, it is a species of concern (US Fish and Wildlife Service) and populations are declining throughout its range (Rinne and Miller 2006). If fish abundance or size distributions change, this could affect the retentiveness of CPOM and creation of habitat structures in soft sediments, which have considerable direct and indirect effects on these ecosystems (Chapter 1).

We expect that depressions will make an important contribution to near bed flows and particle retention under low to moderate flow conditions, but those effects will diminish at high flows. At low to moderate flows, bed load transport is expected to be the more common form of particulate transport. As flow rates increase, higher stresses will increase suspended load transport, decreasing the amount of debris available for deposition. Higher flow rates will also decrease interaction time between a depression and particle, further reducing deposition rates (Yager et al. 1993). Under baseflow conditions in the Gila River, transitionally rough flow is expected, suggesting the divots will concentrate CPOM unless the discharge increases significantly and fully rough flow develops. Our laboratory results are consistent with this

hypothesis and suggest that inertial effects are the physical mechanism responsible for this concentration. Field data shows that the divots significantly increase roughness, suggesting that the feeding behavior of these fish consequently increases turbulence and mass transport.

Small changes to flow patterns near the bed can have important implications for the suitability of habitat for invertebrates and retention of particulate matter, which is also entrained in the fine sediments in general. Our results indicate that divot formation may modify fish-invertebrate interactions from a strictly predator-prey relationship to one where consumption of invertebrates is potentially offset by habitat creation. Sonora suckers (Chapter 2 and 3) range widely and do not necessarily return to the same divot bed to feed, although they do actively forage in existing divots. Therefore we could argue that divot formation is not simply a byproduct of fish feeding activities, but that the creation of divots enhances resource accumulation in feeding habitats, and also possibly attracts prey, which could be a fortuitous coincidence for the foraging fish or an adaptive strategy.

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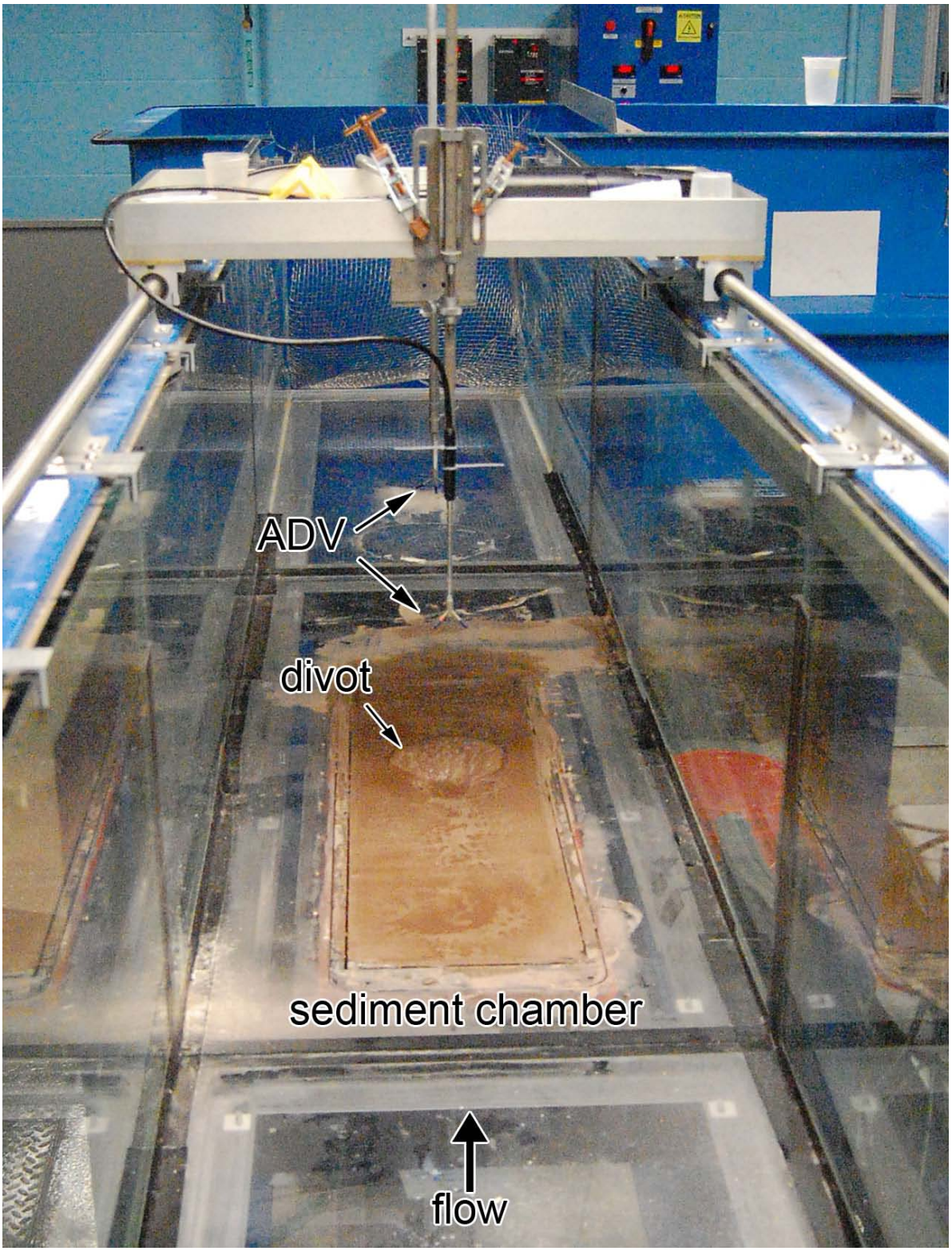

Figure 1. Experimental setup for flume experiments. A divot was created in the sediment chamber, and two Vectrino ADVs were placed above the sediment core, the upstream ADV was located above smooth sediment and the downstream directly above the center of the divot.